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1 Jos M. Milner
2 Hedmark University College
3 Department of Forestry & Wildlife Management,
4 Campus Evenstad, NO-2480 Koppang, Norway.
5 Tel: +44 13397 53854
6 jos.milner@gmail.com

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8 **To Feed or Not to Feed? Evidence of the Intended and Unintended Effects of**
9 **Feeding Wild Ungulates**

10 JOS M. MILNER¹, *Hedmark University College, Department of Forestry and Wildlife*
11 *Management, Campus Evenstad, NO-2480 Koppang, Norway & School of*
12 *Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24*
13 *2TZ, U.K.*

14 FLORIS M. VAN BEEST, *Department of Bioscience, Aarhus University,*
15 *Frederiksborgvej 399, Roskilde 4000, Denmark.*

16 KAROLINE T. SCHMIDT, *Dr. Moritz Zandergasse 7, 2380 Perchtoldsdorf, Austria.*

17 RYAN K. BROOK, *Department of Animal and Poultry Science & Indigenous Land*
18 *Management Institute, College of Agriculture and Bioresources, University of*
19 *Saskatchewan, 51 Campus Drive, Saskatoon, SK S7N 5E2, Canada.*

20 TORSTEIN STORAAS, *Hedmark University College, Department of Forestry and*
21 *Wildlife Management, Campus Evenstad, NO-2480 Koppang, Norway.*

22

23 **ABSTRACT** Ungulate populations are important natural resources, associated with both
24 costs and benefits. Conflicts have arisen between stakeholders who benefit from high
25 ungulate numbers and those faced with the costs. Supplementary or diversionary feeding

¹jos.milner@gmail.com

26 may potentially mitigate conflicts while maintaining harvest yields but can have
27 conservation implications. We quantified the empirical evidence for whether the intended
28 effects, and hence management goals, of feeding are met. We also examined whether any
29 potential unintended consequences of feeding occur and under what conditions. We
30 found clear evidence that supplementary feeding enhanced reproduction and population
31 growth under certain conditions. By contrast, we found limited evidence of the
32 effectiveness of diversionary feeding to protect crops, forestry, and natural habitats, with
33 positive effects often undermined by increases in ungulate density. However, the use of
34 diversionary feeding to reduce traffic collisions seems promising but requires further
35 investigation. The unintended effects of feeding are typically complex, involving changes
36 to demography, behavior and vegetation with consequent cascading effects on other
37 trophic levels, as well as exacerbated risks of disease transmission. Increased ungulate
38 density is the primary driver behind these unintended effects, the consequences of which
39 tend to increase with longevity of feeding and affect a range of stakeholders. We urge
40 managers to take seriously the risks as well as the economic and ethical issues before
41 deciding to feed ungulates.

42

43 **KEY WORDS** artificial feeding, deer, forest damage, habitat impact, herbivore, hunting,
44 supplemental feed, sustainable management, vehicle collision, wildlife disease.

45

46 **INTRODUCTION**

47 Large ungulates are keystone species in many ecosystems and are a highly valued natural
48 resource for social, cultural, and economic reasons (Gordon et al. 2004). Many

49 populations have grown over recent decades, causing environmental and socio-economic
50 impacts on wider communities and conservation concerns, as well as density-dependent
51 changes in performance (Côté et al. 2004, Putman et al. 2011). Consequently, conflicts
52 arise between stakeholders who benefit economically from high ungulate numbers (e.g.,
53 hunters, outfitters, tourism operators) and those faced with the costs of their presence
54 (e.g., land managers, conservationists, transport users and operators; Austin et al. 2010).
55 Manipulating forage availability through the provision of additional food could
56 potentially be a means of mitigating this conflict while maintaining hunter harvest yields
57 and hence rural incomes (Brown and Mandery 1962, Smith 2001). However, some
58 stakeholders have concerns over the sustainability of this management practice and its
59 potentially undesirable ecological side effects (Mysterud 2010, Martínez-Abraín and Oro
60 2013).

61 Wildlife can be fed by humans in many different ways, intentionally (e.g., at
62 feeding stations) and unintentionally (e.g., unprotected agricultural crops and rubbish
63 dumps; Oro et al. 2013, Sorensen et al. 2014). In this review, we focus on the effects of
64 intentional feeding of ungulates, specifically considering supplementary feeding (often
65 called winter feeding) and diversionary, or intercept, feeding used to attract animals away
66 from vulnerable vegetation, livestock, or major traffic arteries (defined fully in
67 Supplemental Material). However, many of the issues raised also apply across a broad
68 range of unintentional but predictable anthropogenic food subsidies (Oro et al. 2013).
69 Earlier reviews of the consequences of feeding large herbivores, published a decade or
70 more ago, found equivocal evidence of its effectiveness (Peek et al. 2002, Putman and
71 Staines 2004). Since then both the scale and extent of feeding have increased (Tarr and

72 Pekins 2002, Bartoskewitz et al. 2003, Mysterud 2010), along with a greater awareness
73 and research focus on its unintended consequences (Inslerman et al. 2006). We therefore
74 summarize the findings of ungulate feeding studies with the aim of establishing 1) the
75 effectiveness of feeding programs, 2) the conditions under which management goals are
76 likely to be achieved, and 3) the conditions under which unintended effects are most
77 likely to occur.

78 **METHODS**

79 We reviewed articles in the peer-reviewed and, to a lesser extent, grey literature that
80 provided empirical evidence of the effects of feeding ungulates throughout the world. We
81 used ISI Web of Knowledge and Google Scholar to identify articles. The search terms,
82 using Web of Knowledge syntax, were (supplement* OR diversion OR intercept OR
83 artificial) AND (feed* OR forag*) and we refined results by (bison OR boar OR deer OR
84 elk OR moose OR ungulate). We manually excluded studies of farmed populations of
85 ungulates. Adding relevant papers and reports cited in key articles but not picked up by
86 our search terms resulted in 232 articles.

87 We identified 5 major management goals of supplementary and diversionary
88 feeding and considered the intended effects of feeding that would allow these goals to be
89 achieved (Table 1). We also identified commonly perceived unintended or secondary
90 consequences of feeding (Table 2). We quantified the evidence for the occurrence of
91 intended and unintended effects and collated information on the conditions under which
92 they occurred. In our analysis of the evidence, we only included controlled studies in
93 which there was variation in the amount of feed provided over time or space, or in which
94 comparisons were made between treatment (fed) and control (unfed) groups, or before

95 and after feeding started or ended ($n = 101$). These studies came from North America (48
96 studies), Fennoscandia (25), or elsewhere in Europe (28) and focused on 9 different
97 ungulate species (Supplemental Material Fig. S1, Tables S1–4). As the implementation of
98 feeding programs likely influences their outcome, we recorded the type of feed provided
99 (i.e., concentrates: fruits, root crops, grain, maize (corn), or pelleted concentrates; bulk
100 feeds: pelleted or unprocessed bulk forage crops including silage, hay, and other
101 roughage) and feed distribution method (feeder units [e.g., hoppers, gravity feeders,
102 troughs], bales of bulk crops, piles of feed or bait, feed spread on ground in lines or
103 scattered) where this information was given (Supplemental Material Fig. S1). We also
104 recorded how long the program had been running. Other factors such as the length of the
105 feeding season, the proportion of the population using supplementation, the quantity of
106 feed provided, and the density or spatial distribution of feeding stations are also likely to
107 be important but were often not reported.

108 We examined whether or not there was evidence of an effect of feeding using
109 logistic regression, assuming a binomial distribution (0: no evidence or evidence in the
110 opposite direction to intended or predicted; 1: evidence in the intended or predicted
111 direction). Explanatory variables were the effect type (intended or unintended),
112 management type (supplementary or diversionary feeding), feed type and distribution
113 method (both classified above), feeding program history (short: < 5 yr; medium: 5–20 yr;
114 long: > 20 yr) and their interactions.

115 **RESULTS**

116 We found stronger evidence of the intended effects of supplementary than diversionary
117 feeding (supporting evidence found in 63.4% and 34.4% of studies, respectively; $\chi^2_{1,101} =$

118 7.54; $P = 0.006$). Furthermore, evidence supported the occurrence of unintended effects
119 more often than intended effects ($\chi^2_{1,168} = 7.29$; $P = 0.007$) and among unintended effects,
120 the probability of occurrence increased with duration of the feeding program ($\chi^2_{2,50} =$
121 6.19; $P = 0.045$). An effect of fewer unintended effects when feeding concentrates ($\chi^2_{2,61}$
122 = 9.71; $P = 0.008$) arose because concentrates were often associated with short-term
123 feeding programs (Supplemental Material Fig. S1). Otherwise, we found no significant
124 effects of feed type, distribution method, or program duration, but this may be partly
125 because of low sample sizes or the disproportionate representation of some study
126 systems.

127 **Effectiveness in Meeting Management Goals**

128 *Improved performance.*—Ecological theory suggests that an increase in the
129 availability of food resources would lead to improved body condition and consequently
130 increased survival and reproductive rates (Bayliss and Choquenot 2002). Indeed these are
131 the intended effects of many supplementary feeding programs (Table 1). Despite this,
132 Putman and Staines (2004) reported relatively little effect of feeding on demographic
133 factors in deer. In contrast, by restricting our evidence to that of case-controlled studies,
134 we found stronger evidence of increased performance under certain conditions (Table 1).
135 A high population density relative to nutritional carrying capacity is one such condition,
136 with performance gains being more likely when supplementary feed is provided to a
137 population with poor natural forage resources (Tarr and Pekins 2002, Bartoskewitz et al.
138 2003).

139 Performance gains are less likely to be detected if there is a mismatch between the
140 season in which feed is provided and the season in which demographic parameters are

141 measured. We found evidence that feeding during winter reduced natural overwinter
142 mass loss or loss of condition in 5/7 studies (Table 1), with enhanced body reserves likely
143 providing an insurance against extreme winter conditions (Fauchald et al. 2004, Bårdsen
144 et al. 2008). By contrast, no studies ($n = 7$) showed a clear effect of winter feeding on
145 carcass weights the following autumn or hunting season (Table 1). Autumn mass is
146 generally more dependent on the quality of summer foraging conditions that replenish
147 body reserves after winter, than on conditions during the previous winter (Parker et al.
148 2009, Cook et al. 2013). However, where animals are provisioned year-round (typically
149 in mediterranean climates [e.g., Texas and Spain]; Olguin et al. 2013) or winter
150 supplementary feeding begins in autumn (Bartoskewitz et al. 2003), autumn weights may
151 increase, particularly among yearlings and males (3/4 studies; Supplemental Material
152 Table S1).

153 Among adult females, an effect of feeding is complicated by the strong impact of
154 reproductive status on autumn mass (Cook et al. 2013). Where resources from winter
155 feeding are largely allocated to reproduction rather than somatic growth (e.g., Bårdsen et
156 al. 2008, Milner et al. 2013), greater energetic investment in lactation during the summer
157 can lead to lower autumn mass among fed than unfed adult females with fewer or no
158 offspring (Bårdsen et al. 2009, van Beest and Milner 2013). Consequently, offspring of
159 supplementally fed females are often heavier (Table 1) because of increased milk yields
160 and higher neonatal growth rates (Jacobsen et al. 1981, Smith et al. 1997).

161 The reproductive rate (number of offspring per adult female in summer or
162 autumn) of supplementally fed herbivores increased in 5/7 studies (Table 1). In those
163 studies showing clear positive effects, population density was generally high or

164 increasing relative to the natural forage availability (e.g., Milner et al. 2013). Under such
165 circumstances, feeding can provide a buffer against the adverse effects of density and
166 environmental stochasticity on the life-history traits of adult females (Rodriguez-Hidalgo
167 et al. 2010, Ballesteros et al. 2013). Where reproductive rate is already naturally high,
168 feeding is not likely to increase it further (e.g., 92% calving in semi-domesticated
169 reindeer; Fauchald et al. 2004).

170 The effects of feeding on survival tend to be weak, particularly in adults, which
171 have naturally high overwinter survival. Improved survival occurs primarily among
172 juveniles (Ozoga and Verme 1982, Smith and Anderson 1998) and in severe winters
173 (Lewis and Rongstad 1998, Tarr and Pekins 2002, Fauchald et al. 2004), particularly
174 where individuals congregate on degraded winter ranges (Peterson and Messmer 2007).
175 In heavily hunted populations where density is kept below habitat carrying capacity,
176 natural winter mortality tends to be low, thus constraining any survival benefit of feeding
177 (Lewis and Rongstad 1998). Ultimately the effectiveness of feeding programs to improve
178 performance at the population level depends on the proportion of individuals using the
179 feed (Bartoskewitz et al. 2003). For example, a low proportion of female white-tailed
180 deer (*Odocoileus virginianus*) used supplementary summer feed in a study in Texas that
181 showed no significant effect of feeding on female body mass, whereas a high proportion
182 of males used the feed resulting in significant effects on antler size and mass of some age
183 classes (Bartoskewitz et al. 2003).

184 *Compensation for loss of range.* —Although many feeding programs, particularly in
185 North America, state compensation for loss or fragmentation of natural winter range as
186 their rationale (Smith 2001, Peterson and Messmer 2011), few controlled studies ($n = 3$)

187 reported the effects of feeding on carrying capacity (Supplemental Material Table S1). At
188 the population level, we would expect that feeding increases nutritional carrying capacity
189 and therefore population density, if other factors are not limiting (Brown and Cooper
190 2006, Oro et al. 2013). This reduces the effects of density dependence (Lubow and Smith
191 2004), and population growth rates may increase (e.g., Ballesteros et al. 2013) until a new
192 higher carrying capacity is approached (Ozoga and Verme 1982). Although our findings
193 supported this pattern (Table 1), feeding programs also have the potential to decrease
194 carrying capacity at high densities, either through negative impacts on summer or autumn
195 forage availability (Ozoga and Verme 1982) or through an increase in year-round use of
196 limited winter ranges because of changes in migration patterns (Peterson and Messmer
197 2011).

198 *Increased hunting and viewing opportunities.*—Feeding is expected to increase
199 hunting and game viewing opportunities either as a result of higher hunting quotas based
200 on larger ungulate population sizes or through increased encounter rates. The latter may
201 result from either an increase in population size or density, or through changes in spatial
202 behavior which increase aggregation or spatial predictability of game species. The latter
203 underlies the practice of baiting by hunters (van Deelen et al. 2006) and can keep game
204 within a desired hunting ground, eventually disrupting the tradition of migration under
205 long-term feeding (Peek et al. 2002).

206 As indicated above, population density often increases as a result of feeding
207 (evidence from 4/6 studies; Table 1). We also found strong evidence that the provision of
208 additional forage at focal points in the landscape alters the distribution and natural
209 foraging behavior of animals, leading to increased local densities and aggregations

210 around feeding stations (Table 1). Indeed, 8/8 studies observed a shift in activity center or
211 core area within the home range towards feeding stations (e.g., Cooper et al. 2006, Webb
212 et al. 2008), while a further 2 studies showed increased local density and group size
213 (Sánchez-Prieto et al. 2004, Pérez-González et al. 2010).

214 Despite these intended effects being met, the evidence that they led to higher
215 hunter success was weak (Table 1). Although a number of North American studies have
216 reported increased hunting success of fed or baited white-tailed deer (see Dunkley and
217 Cattet 2003, Inslerman et al. 2006), the differences in harvest rates between hunters using
218 and not using bait were often small and not tested statistically (e.g., Winterstein 1992). Of
219 4 controlled studies, 1 showed a significant improvement in hunting success (Table 1;
220 Supplemental Material Table S1). Baiting was most effective among archery hunters who
221 require closer proximity to the animal for success (van Deelen et al. 2006, Kilpatrick et
222 al. 2010). Other studies suggested that baiting neither improved hunter success nor
223 increased landscape-level deer harvests (van Deelen et al. 2006, Tardiff Fleegle and
224 Rosenberry 2010), although where a baiting ban reduces hunter numbers, the total harvest
225 may decrease (Rudolph et al. 2006).

226 *Reduced vehicle collisions.* —The use of diversionary feeding to reduce collisions is
227 based on an expected alteration of the movement and spatial distribution of animals. For
228 example, animals may be intercepted during migration or their movement and ranging
229 behavior restricted. However, evidence that feeding alters migratory behavior of
230 ungulates was equivocal (3/5 studies; Table 1). Winter feeding in Scandinavia was unable
231 to halt moose (*Alces alces*) migration early in the migration phase (Sahlsten et al. 2010),
232 although feeding stations close to the end of migration routes and within wintering areas

233 were used (Gundersen et al. 2004, Sahlsten et al. 2010). This contrasts with the disruption
234 of migration under long-term feeding in red deer (*Cervus elaphus*) on hunting grounds
235 (Peek et al. 2002). Where feeding does not alter migration, spatial and seasonal variation
236 in nutritional carrying capacity and predation risk seem to be more important
237 determinants of migratory behavior (Mysterud 1999, White et al. 2010).

238 Evidence of restricted ranging was even weaker with 3/8 studies showing that
239 feeding reduced total home range size (Table 1), whereas other cases showed increased or
240 unchanged home range size after the initiation of feeding (Supplemental Material Table
241 S2). This is presumably due to the need to meet other resource requirements (Brown and
242 Cooper 2006). For example, the use of cover to mediate unfavorable weather conditions
243 or reduce predation risk also strongly influences spatiotemporal behavior (Merrill et al.
244 2010, van Beest and Milner 2013).

245 When habitat requirements other than forage are limiting around feeding stations,
246 animals may actually increase their movement and adjust their space use or habitat
247 selection to meet those needs (Webb et al. 2008). Although movement rates of white-
248 tailed deer and Angora goats (*Capra hircus*) did not change after being offered
249 supplemental feed (Murden and Risenhoover 1993), moose using feeding stations moved
250 more than non-users (Mathisen et al. 2014) and fed mule deer (*Odocoileus hemionus*)
251 moved farther from bed sites to feed (Peterson and Messmer 2011). In Alpine areas, red
252 deer that were fed in thermally unfavorable valley bottoms for practical reasons, moved
253 daily to the better thermal conditions of high elevation meadows, whereas non-
254 supplemented herds remained in alpine meadows throughout winter (Schmidt 1993).
255 Nonetheless, although supplementary feeding does influence the distribution and habitat

256 selection process of individuals, its effects appear to be largely restricted to small spatial
257 and temporal scales (Pérez-González et al. 2010, van Beest et al. 2010b).

258 Evaluations of mitigation efforts to reduce animal-vehicle collisions are
259 widespread in the literature (e.g., Groot Bruinderink and Hazebroek 1996, Huijser et al.
260 2009), but few case studies have explicitly considered diversionary feeding (Table 1).
261 There were 3 exceptions. In an area of high mule deer vehicle collisions, mortality due to
262 collisions was similar in fed and unfed sites but was offset by increased productivity at
263 the fed site (Peterson and Messmer 2011). Wood and Wolfe (1988) showed that feeding
264 mule deer reduced vehicle collisions sufficiently to be economically beneficial although
265 reductions were only significant in 2/6 trials. Andreassen et al. (2005) found that 3
266 mitigation measures combined (forest clearing, feeding, predator scent) reduced moose–
267 train collisions by 46%. Both of the latter studies recommended further investigations
268 into the effectiveness of diversionary feeding to reduce collisions, but none has occurred
269 to date.

270 *Reduced damage to crops, forestry, and natural vegetation.* —Diversionary feeding
271 may be used as a tool to reduce or prevent herbivore impacts on vegetation or habitats of
272 high commercial or conservation value, either by altering the distribution of ungulates
273 across the landscape or by altering their diet or habitat selection patterns. The
274 effectiveness of feeding in controlling spatial distribution is described above and was
275 found to be unclear. In terms of changing diet, we would intuitively expect that providing
276 herbivores with additional forage should decrease their reliance on natural vegetation and
277 reduce impacts on the environment (Schmitz 1990, Kowalczyk et al. 2011). However,
278 empirical evidence shows that many supplementally fed herbivores continue to forage on

279 natural vegetation, some without notable changes in their natural diet (e.g., Schmitz 1990,
280 Doenier et al. 1997, Cooper et al. 2006, van Beest et al. 2010a). The only study to
281 consider whether diversionary feeding altered habitat use found no difference between
282 feeding site users and non-users (van Beest et al. 2010b).

283 Of 16 controlled studies, 6 showed diversionary feeding to be effective in
284 reducing damage in the targeted areas, whereas 4 showed a significantly increased
285 impact, opposing the management goal (Table 2). Efficacy was related to the type of feed
286 provided, the proximity of feeding sites to vulnerable vegetation, the longevity of the
287 feeding program, and its effects on population density. Nonetheless, managers may
288 perceive diversionary feeding to be effective where there are economic benefits,
289 regardless of the ecological outcome. For example, the reduction in damage to French
290 vineyards by wild boar (*Sus scrofa*) as a result of diversionary feeding was sufficient for
291 savings in compensation payments to be made, despite a statistically non-significant
292 reduction in damage (Calenge et al. 2004).

293 Feed type in relation to the grazing or browsing strategy of the target species
294 along the continuum from bulk roughage feeders to concentrate selectors, seems to
295 influence effectiveness (Table 1). For example, providing silage and hay successfully
296 reduced agricultural damage and browsing in European bison (*Bison bonasus*), a bulk
297 feeder (Kowalczyk et al. 2011), but did not reduce forest damage by moose, a concentrate
298 selector (van Beest et al. 2010a, Mathisen et al. 2014). Forestry residues are potentially a
299 more effective feed type for reducing moose forest damage but have yet to be formally
300 tested (Månsson et al. 2010). Low-fiber concentrates fed to mixed feeders such as elk
301 (*Cervus canadensis*) and red deer increased the utilization of winter pasture (Kozak et al.

302 1994) and may reduce bark damage (Rajský et al. 2008), whereas high-fiber bulk diets
303 reduced grazing pressure (Kozak et al. 1994). Concentrates fed to white-tailed deer
304 (concentrate selectors) increased the proportion of natural browse in the diet in spring and
305 forbs in autumn but had no effect on forage choices in summer or winter (Timmons et al.
306 2010). Natural forage may be required to balance a shortage of essential nutrients in the
307 supplemental feed (Schmitz 1990), or stimulate the digestive tract to alleviate the risk of
308 ruminal acidosis (Timmons et al. 2010).

309 More generally, feeding may exacerbate the scale of vegetation damage by
310 contributing to ungulate population growth so increasing density and undermining any
311 potential diversionary benefits. This is especially true for species with a high
312 reproductive capacity such as wild boar (Bieber and Ruf 2005, Imesch-Bebié et al. 2010),
313 and has been observed where long-term feeding (>20 yr) was associated with a high
314 landscape-scale browsing impact as moose population density increased relative to
315 natural forage availability (Mathisen et al. 2014).

316 **Evidence of Unintended Effects of Feeding**

317 *Altered population dynamics.* —Besides the intended demographic effects of feeding,
318 there may be unintended demographic and evolutionary effects but in general these have
319 been less well studied (Table 2). For example, density dependence may be reduced
320 (Lubow and Smith 2004) with consequences for population dynamics. Consequently, we
321 expected that feeding would lead to a reduction in variance in population size. However,
322 we found no studies that formally addressed this (Table 2), although Boyce (1989) noted
323 that fluctuations in the size of the Jackson elk herd were lessened, reducing the dynamic
324 nature of the ecosystem.

325 *Genetic effects and changes to selection.* —Feeding may affect the genetic structure
326 of populations. Spatial homogeneity of allele frequencies was increased in supplementally
327 fed white-tailed deer with the loss of microgeographic genetic structure normally
328 associated with kin-structured social groups (Blanchong et al. 2006). Feeding may also
329 reduce selection pressures on nutrition-mediated traits such as overwinter mortality
330 (Schmidt and Hoi 2002) and reproductive success (Rodriguez-Hidalgo et al. 2010) by
331 buffering individuals against the effects of environmental variation. Some overwinter
332 mortality may be considered beneficial because it maintains natural selection against poor
333 quality individuals (Boyce 1989). Supplementally fed red deer calves and yearlings
334 showed higher intra-cohort variation and lower inter-cohort variation in body weight than
335 among non-supplemented red deer, implying that fed individuals may be under reduced
336 natural selection pressure during their first year of life (Schmidt and Hoi 2002). However,
337 there are no studies that explicitly examine the effects of feeding on natural selection, the
338 evidence from red deer being circumstantial and likely distorted by selective hunting
339 (Mysterud 2011).

340 Feeding may also affect sexual selection by increasing the variance in male
341 mating success among polygynous species. Sánchez-Prieto et al. (2004) showed that
342 spatially clumped feeding led to high aggregation of females and greater variance in
343 harem sizes of red deer. This shows that feeding during the rut can increase the degree of
344 polygyny, but no studies have explicitly measured male reproductive success in relation
345 to feeding (Table 2).

346 *Altered behavior.* —Providing additional forage at focal points in the landscape clearly
347 affects the spatial behavior of animals (Table 1). The concentrated activity and movement

348 of animals around feeding stations described above match the predictions of central-place
349 foraging theory (van Beest et al. 2010b). Such aggregation has consequences for social
350 behavior, as well as inter- and intra-specific interactions and stress levels. Aggression
351 (Donohue et al. 2013) and stress (Forristal et al. 2012) both increase with ungulate
352 density, and 4/5 studies observed higher levels of aggression associated with feeding
353 (e.g., Pérez-González et al. 2010).

354 Aggressive interactions and access of subordinates to supplemental feed vary
355 seasonally (Ozoga and Verme 1982) and particularly with the way in which feeding is
356 implemented in terms of feed type and its temporal and spatial distribution (Schmidt et al.
357 1998, Schmidt and Hoi 1999). Interference competition generally increases with
358 increasing spatial clumping of resources. For example, a clumped feed distribution
359 provided to red deer during the rut led to higher rates of male-male interaction and male
360 harassment of females than a dispersed feed distribution, although females experienced
361 lower per capita harassment because of larger harem sizes (Sánchez-Prieto et al. 2004).
362 Nonetheless, aggressive interactions are not always sufficient to result in interference
363 competition (Veiberg et al. 2004). Patch size, profitability and depletion rate influence
364 the extent of interference competition and aggression, particularly among subordinate
365 males which may avoid using feeding sites if patch profitability is too low for efficient
366 participation (Schmidt et al. 1998). Interspecific spatial avoidance may also occur, as
367 observed where moose and red deer used feeding stations in the same areas (Johnsen
368 2012).

369 *Impacts on vegetation and habitats.* —Where vegetation is not protected by snow in
370 winter, patterns of habitat or range degradation associated with ungulate feeding can be

371 similar to those observed around artificial water holes used by domestic livestock
372 (Andrew 1988). Habitat impacts include changes in plant composition and diversity due
373 to increased browsing pressure on woody dwarf shrubs (Mathisen et al. 2010) and trees
374 (Smith et al. 2004), a consequent loss of understory cover (Pedersen et al. 2014), and an
375 increase in light-demanding species and grasses (Mathisen et al. 2010). Evidence of all
376 these effects has been documented (Table 2), but they occur primarily as consequences of
377 an increase in local herbivore density rather than a direct consequence of feeding. Few
378 studies tease these factors apart, with the input of nutrients being an important additional
379 factor at feed sites (Mathisen and Skarpe 2011).

380 In studies addressing the increased probability of browsing or grazing impacts in
381 response to feeding (4/4 studies; Table 2 and Supplemental Material Table S3), such
382 effects were typically strongest in the immediate vicinity of feeding stations and
383 weakened with increasing distance from feeding stations (van Beest et al. 2010a).
384 Increased utilization (Peterson and Messmer 2011) or depletion (Cooper et al. 2006, van
385 Beest et al. 2010a) of preferred natural forage species is commonly found in areas with
386 feeding, with the extent being determined by feeding history, as well as the quantity and
387 quality of the provided feed (Brown and Cooper 2006, Kowalczyk et al. 2011). Indeed,
388 the area over which impact on the natural vegetation occurs can increase considerably
389 with feeding program duration and may be sustained by re-browsing for a number of
390 years after feeding stations cease operating (van Beest et al. 2010a). Nonetheless,
391 landscape heterogeneity may allow the regeneration of preferred species despite close
392 proximity to feeding sites and high herbivore densities, particularly in species such as
393 aspen (*Populus tremuloides*) with episodic regeneration (Barnett and Stohlgren 2001).

394 Supplementary feeding of free-ranging ungulates is often practiced in natural
395 habitats and as such poses a risk of introducing exotic weed species into native
396 ecosystems (Rinella et al. 2012), which can be further dispersed by wind, birds, or
397 mammals. Feed products such as hay bales, oilseeds, cereals, and pulse crops are
398 generally contaminated with seeds of a variety of weed species. Even processed feeds
399 such as pellets made from hay and grain may contain viable weed seeds (Cash et al.
400 1998). These seeds can sometimes survive for years or decades before germinating
401 (Lewis 1973). Ungulates can disperse seeds of exotic and native species widely
402 (Bartuszevige and Endress 2008), with viable weed seeds found in the feces from
403 ruminants for days after consumption (Wallander et al. 1995, Jaroszewicz et al. 2009).
404 Furthermore, colonization by exotic invasive plant species is facilitated by reduced
405 competition from heavily browsed native vegetation (Rinella et al. 2012) and soil
406 disturbance in areas of concentrated activity at feeding sites (MacDougall and Turkington
407 2005). Despite an increasing awareness of the role played by ungulates in spreading seeds
408 (Bartuszevige and Endress 2008, Picard and Baltzinger 2012), we found only 2
409 documented cases, both from the Greater Yellowstone Ecosystem, USA, where the
410 spread of invasive plant species was directly attributable to feeding (Table 2). A third
411 study showed a slightly higher species diversity, proportion of synanthropic species, and
412 number of seedlings per dung sample in supplementally fed than unfed groups of
413 European bison, although differences were not significant (Jaroszewicz et al. 2009).

414 *Impacts on other taxa.* —Feeding has both direct and indirect effects across whole
415 ecosystems by altering patterns of herbivory and nutrient input (Mathisen and Skarpe
416 2011). These factors alter the competitive balance between species and hence community

417 composition, which in turn can have cascading effects through the trophic levels. Much
418 research effort has focused on the negative impacts on biodiversity and species richness
419 of sustained heavy grazing and browsing (Fuller and Gill 2001, Côté et al. 2004, Foster et
420 al. 2014) without considering the potential balancing effects of nutrient input due to
421 feeding (Mathisen and Skarpe 2011). Although feeding affected the composition of small
422 mammal (Pedersen et al. 2014) and passerine bird (Anderson 2007, Mathisen and Skarpe
423 2011) communities, only 1 of these 3 studies reported a reduction in species richness
424 (Table 2); shrub-steppe bird species were favored at the expense of woodland species
425 (Anderson 2007). Overall biodiversity may be unaffected if species replacement occurs,
426 although species with a high conservation value may be replaced by more common,
427 generalist species, potentially leading to biotic homogenization (Olden 2006).

428 Species' responses to feeding depend on their functional groups (Mathisen and
429 Skarpe 2011) or on environmental conditions (Moseley et al. 2011). For example, seed-
430 eating bird species responded positively to browsing but negatively to feeding stations
431 (Mathisen and Skarpe 2011), whereas the response of insect-eating bird species depended
432 on arthropod prey type (Pedersen et al. 2007, Mathisen et al. 2012). The effects of
433 feeding on rodent abundance were small in an area of high climatic stochasticity
434 (Moseley et al. 2011) and smaller than the inter-annual variation in cyclic populations
435 (Pedersen et al. 2014). Where feeding reduces herbivore winter mortality, scavengers
436 reliant on carcasses could also be affected (sensu Oro et al. 2013).

437 Feeding stations often attract non-target species such as raccoons (*Procyon lotor*),
438 collared peccaries (*Pecari tajacu*), skunks and rodents, particularly where grain or maize
439 (shelled corn) are provided and accessible to these species (Cooper and Ginnett 2000,

440 Moseley et al. 2011, Campbell et al. 2013, Selva et al. 2014). Consequently unnaturally
441 high intra- and inter-specific contact rates can occur around feeding sites (Campbell et al.
442 2013). Nest predation of, for example, freshwater turtles or ground-nesting birds may
443 increase around feeding stations because of the attraction of nest predators if feeding
444 occurs during the nesting season (Cooper and Ginnett 2000, Hamilton et al. 2002). In
445 addition, issues may arise where provided feed is toxic to non-target species. For
446 example, 20% of deer corn sold in Texas had levels of aflatoxin that would be toxic to
447 birds and other non-target species (Brown and Cooper 2006). Of 7 controlled studies, 6
448 showed an impact of feeding on non-target species (Table 2).

449 *Effects on parasite and disease transmission risk.* —Naturally occurring diseases and
450 parasites are widespread in wildlife populations and most have minimal overt impacts on
451 populations. However, several key diseases, especially emerging infectious diseases, are
452 widely recognized as threats to conservation, agriculture and public health worldwide
453 (Gortázar et al. 2006, Jones et al. 2008). We expected that feeding ungulates would
454 promote parasite and disease transmission either by increasing direct transmission
455 through interactions such as sneezing, coughing, nose-to-nose contact or sparring (Garner
456 2001, Miller et al. 2006), or by indirect transmission through infectious materials in the
457 environment (Creech et al. 2012). These include shared feeds contaminated by body
458 fluids from an infectious animal (Palmer et al. 2004). We found strong evidence that
459 feeding can significantly enhance disease transmission, including some diseases that have
460 important impacts on wildlife populations (10/14 studies; Table 2). However, the
461 likelihood of feeding enhancing transmission depends on the life-history of pathogens
462 (Vicente et al. 2007; Table 2) and their ability to survive in the environment. For

463 example, enhanced transmission is potentially greater in macroparasites with direct rather
464 than indirect life cycles (Navarro-Gonzalez et al. 2013) and in pathogens that are
465 transmitted during the season when feeding occurs (Cross et al. 2007) or have a very high
466 capacity to survive in the environment for months or years such as prions.

467 Processes that increase intra- and inter-specific contact rates, for example by
468 increasing host density or aggregation, have the potential to promote disease transmission
469 (Gortázar et al. 2006, Sorensen et al. 2014). Contact rates of adult female elk were more
470 than twice as high on feeding grounds as elsewhere (Cross et al. 2013); therefore, feed
471 sites may enhance direct and indirect transmission of infectious diseases (e.g., Creech et
472 al. 2012, Campbell et al. 2013). Feeding also increases contact rates with infectious
473 material in the environment such as aborted fetuses on feed grounds where brucellosis
474 (caused by *Brucella abortus*) is prevalent (Creech et al. 2012) or prions in the case of
475 chronic wasting disease (CWD), which has emerged relatively recently in North America
476 (Miller et al. 2006). Nonetheless, seroprevalence of brucellosis has been increasing with
477 elk density in areas both with and without feed grounds in recent years (Cross et al.
478 2010). Lateral transmission and the spread of infectious prions in saliva are also
479 important in the transmission of CWD (Salman 2003, Mathiason et al. 2006).

480 The implementation of feeding programs may affect transmission risks. The
481 quantity of feed provided, number of large feeding sites, provision of fruit and root crops
482 rather than grain, and percentage of sites spreading grain were all associated with
483 increased prevalence of bovine tuberculosis (caused by *Mycobacterium bovis*) in white-
484 tailed deer (Miller et al. 2003). Density of feeder units was more influential than host
485 abundance in explaining infection by gastrointestinal parasites in wild boar, with feeders

486 appearing to act as points of infection (Navarro-Gonzalez et al. 2013). Clumped, high
487 density feed sites are therefore often associated with higher risks than dispersed feed
488 (Miller et al. 2003). However, spreading feed on the ground may increase the risks of
489 parasite transmission through fecal contamination of feed lines (Hines et al. 2007) and
490 fecal ingestion (Thompson et al. 2008). Moreover, Thompson et al. (2008) found that
491 none of the feeding strategies they evaluated (feed was piled or spread on the ground or
492 provided in troughs, either rationed or ad libitum) reduced the potential risk of disease
493 transmission to levels comparable with natural foraging areas.

494 Supplemental feeds have been clearly identified as fomites, which can carry
495 disease in the environment and facilitate indirect transmission to new hosts (Palmer et al.
496 2004, Palmer and Whipple 2006). Key factors influencing the relative effectiveness of
497 disease transmission by this route include the type of feed used, environmental
498 conditions, and the specific disease organism. Agents of diseases such as bovine
499 tuberculosis can survive weeks or months in the environment, whereas prions and
500 endospores of *Bacillus anthracis* which cause anthrax can survive for years or longer
501 (Soparker 1917, Palmer and Whipple 2006). Chronic wasting disease is especially
502 concerning because of its long survival in the environment and on feeds, impacts on
503 ungulate populations, and lack of effective control measures.

504 Although feeding can increase contact rates, it may potentially reduce the
505 susceptibility of hosts to infection by improving body condition (Gortázar et al. 2006).
506 Relatively few studies have considered this, but we found supporting evidence in 2/4
507 cases associated with nematode infection (Table 2). In both cases, feeding likely reduced
508 infection by gastrointestinal (Hines et al. 2007) and extrapulmonary (Vicente et al. 2007)

509 nematodes because nematodes induce a strong and costly host immune response. In
510 contrast, the transmission of mass-acting directly transmitted infectious diseases such as
511 bovine tuberculosis, which induce only low levels of immunity, is likely to be
512 independent of body condition (Vicente et al. 2007).

513 **DISCUSSION**

514 Our review shows that whether or not ungulate feeding is effective in achieving its goals,
515 it often results in unintended effects, with the main drivers being sustained high herbivore
516 densities and/or the long-term concentration of individuals around feeding sites. Where
517 enhanced reproduction and increases in herbivore density or aggregation are the intended
518 effects of management, supplementary feeding may be considered effective, although we
519 did not find clear evidence that winter feeding increases autumn carcass mass (Table 1).
520 By contrast, the evidence that diversionary feeding programs are effective is more limited
521 (Table 1). This is primarily because of the difficulties in controlling animal movement,
522 presumably due to other resource needs or disturbance by humans or predators, and
523 because any beneficial diversionary effects are often undermined by increases in
524 population density.

525 The unintended effects of feeding are generally less well studied (Table 2) so are
526 likely to be more widespread than currently perceived. Many are complex, take time to
527 manifest and act across trophic levels (Timmons et al. 2010, Mathisen et al. 2012),
528 making their full impact difficult to appreciate, especially because of synergistic effects.
529 Where unintended shifts in species composition occur, changes may be considered
530 desirable or undesirable depending on how different species or management outcomes
531 are valued (Minteer and Collins 2005). The genetic, epigenetic, and evolutionary

532 consequences of feeding have barely been considered to date, yet may reveal
533 consequences as marked as those of selective harvesting (Allendorf and Hard 2009, Ciuti
534 et al. 2012) when the required research effort is focused on them. Although the small
535 sample size of studies of some unintended effects preclude drawing conclusions, the
536 balance of currently available evidence across effects suggests that most of the potential
537 unintended effects of feeding do indeed occur (Table 2), particularly under long-term
538 feeding programs. This highlights a genuine cause for concern over the long-term use of
539 feeding programs in many circumstances.

540 Feeding programs are implemented in a wide variety of ways. Although we found
541 no clear patterns to suggest feed type and distribution methods influenced the overall
542 outcome of feeding, this may partly be due to insufficient research and hence low sample
543 sizes. Nonetheless, to reduce the chances of unintended effects of feeding occurring,
544 population densities should be kept under control, although this may not be easy to
545 achieve. As hunting pressure is increased, animals become more shy and stay within
546 cover; hunting or culling at feeding and bait sites can cause them to use these sites at
547 night or not at all (Tardiff Fleege and Rosenberry 2010, Ciuti et al. 2012). It may
548 therefore be appropriate to combine population control with range improvement,
549 manipulation of natural forage availability, and positive and negative behavioral
550 reinforcement within an integrated management approach (Mangus 2011, Reimoser and
551 Putman 2011).

552 **Economic Considerations**

553 Contemporary game harvesting systems have relatively few financial inputs yet can
554 generate considerable income from the sale of hunting opportunities, trophies, or meat

555 where it is legal (Gordon et al. 2004, Olausson and Skonhøft 2011), as well as indirect
556 revenue associated with selling hunting equipment, guiding services, food, fuel, or
557 accommodation (Smith 2001). Consequently, where supplementary feeding allows larger
558 trophies or more animals to be harvested, it can be profitable despite the costs of feeding,
559 even with expensive high quality feeds (Smith 2001, Peek et al. 2002). Large-scale
560 feeding programs are often more cost-effective, whereas considerable financial
561 investment on individual properties may give little return (Putman and Staines 2004,
562 Page and Underwood 2006).

563 However, high ungulate densities associated with large feeding programs may
564 lead to considerable risks and indirect costs (Smith 2001). These are typically borne by
565 different stakeholders to those receiving the benefits, or by the wider society. Examples
566 are those related to the control of disease (Daszak et al. 2000) or invasive weeds
567 (Pimentel et al. 2005), damage to forestry or crops (Reimoser and Putman 2011), and the
568 infrastructure required to prevent landslides or avalanches in degraded habitats.
569 Ecological costs such as the loss of migration routes or biodiversity impacts are less
570 tangible and particularly difficult to assign monetary values to (Wallace 2007). Both the
571 costs and risks are likely to increase with the scale and duration of feeding, and may be
572 time-lagged, whereas benefits occur immediately.

573 On the other hand, if ungulate feeding is successful in terms of reducing vehicle
574 accidents, it could have important socio-economic benefits to society (Wood and Wolfe
575 1988, Andreassen et al. 2005) as well as animal welfare (Olausson and Skonhøft 2011).
576 Although the effectiveness in reducing collisions is not well studied, even limited success
577 might be economically and morally justifiable where high material costs and loss of life

578 occur. Two studies suggested that diversionary feeding may reduce collisions by up to
579 40%, with benefits exceeding costs in 1 case (Wood and Wolfe 1988). Further research is
580 needed in this area, particular in terms of diverting animals without causing population
581 increases.

582 **Ethical Issues**

583 Wildlife is heavily affected by anthropogenic activities, particularly climate and land use
584 change, creating ethical obligations for wildlife and conservation managers (Minteer and
585 Collins 2005). Attitudes towards wildlife and these obligations vary over time, regionally
586 and between interest groups, and are reflected in national and international laws. The
587 result is a gradient of management intervention from unmanaged wildlife, through
588 intensively managed wildlife and game ranching, to the extreme of farmed or captive
589 wildlife (Orams 2002, Brown and Cooper 2006). Depending on one's perspective,
590 feeding, together with selective harvesting, fencing, and predator control, may be viewed
591 as either an obligation of hunters in their role as guardians of wildlife, or as steps towards
592 the domestication of ungulates (Brown and Cooper 2006, Mysterud 2010, Schmidt 2014).
593 Feeding comes at the price of taming wildlife, giving rise to public concerns (Butler et al.
594 2005). It can be perceived to de-value wildlife and wildlife habitats (Smith 2001) and
595 contravene the concepts of fair chase and public ownership of wildlife (Brown and
596 Cooper 2006, Inslerman et al. 2006). By shifting wildlife management towards
597 agricultural production, feeding affects hunters' and the public's perceptions of wildlife
598 and the acceptability of natural mortality (Schmidt 2014). Most stakeholders would likely
599 consider the extreme situation in which large game animals only occur in fed populations

600 to be undesirable, but ultimately it is up to society to decide the acceptable extent of
601 intervention.

602 **MANAGEMENT IMPLICATIONS**

603 To feed or not to feed? This is the question that we urge managers to consider fully
604 before implementing feeding programs. Our evidence indicates that unintended effects of
605 feeding are likely when practiced over the long-term, in ways that allow locally high
606 densities of ungulates to occur and when the feed provided does not match that of the
607 foraging strategy of the target species (Table 2). Therefore managers should consider the
608 following points:

- 609 1. To reduce the potential for unintended effects, population densities should be kept
610 below some pre-determined threshold; for example, the natural carrying capacity
611 of the area before feeding. In addition, sufficient natural forage should be
612 available in seasonal ranges occupied outside the feeding season. Population
613 control, ideally carried out during a short and intense hunting season that ends
614 before feeding starts, is also likely to improve the effectiveness of diversionary
615 feeding.
- 616 2. A low density feeding approach may reduce disease spread and is likely better for
617 the surrounding vegetation, although contact rates still tend to be higher than in
618 natural situations (Thompson et al. 2008) and dispersed feeds can also carry
619 infectious organisms. Widely dispersed feed reduces monopolization by a few
620 individuals, improving access by subdominants and reducing stress and
621 aggression.

- 622 3. The feed provided needs to be appropriate to the target species. Natural forage is
623 likely the best option (although this may require further testing; Månsson et al.
624 2010) to limit the attraction of non-target species and dietary changes that
625 indirectly lead to undesired effects. Because the management of invasive species
626 can be extremely costly (Pimentel et al. 2005), the use of certified weed-free
627 forage (North American Invasive Species Management Association 2013) is
628 recommended, particularly in or near protected areas.
- 629 4. Feeding sites should be established in areas away from vulnerable vegetation and
630 disturbance, and where multiple habitat requirements can be met.
- 631 5. Long-term monitoring should be implemented to ensure early detection of
632 unintended effects of feeding such as disease (Sorensen et al. 2014),
633 establishment of invasive species, and habitat impacts. Defensible baselines
634 should also be established prior to implementing feeding.
- 635 6. At the outset, stakeholders should agree who will pay the direct costs of
636 maintaining the feeding program over time and who will pay the costs of
637 unintended effects. Furthermore, the longevity of a feeding program should be
638 considered as the severity of unintended effects may increase over time (e.g., van
639 Beest et al. 2010a). The consequences of stopping feeding and the reversibility of
640 unintended effects are as yet largely unknown (but see Groot Bruinderink et al.
641 2000, Mangus 2011) and will likely require a dramatic reduction in population
642 size to a level that can be supported by the existing natural habitat.

643

644

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649

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Table 1. Intended effects associated with the main management goals of ungulate feeding and the number of empirical studies providing evidence in support of each per the number of relevant studies. We also provide conditions under which intended effects are most likely to occur. Full details of all evidence are provided in Supplemental Material (Tables S1 and S2).

Type of feeding	Management goal	Intended effect	Evidence	Conditions
Supplementary feeding	Improved individual or population performance	Increased survival rate	4 / 7	Low natural survival rates; food-limited populations; severe weather years; fed for entire winter; areas of low disturbance; vulnerable age and sex classes benefit most
		Increased reproductive rate	5 / 8	Low natural reproductive rates; populations close to carrying capacity; summer forage not limiting; sufficient proportion of females fed to give population-level response
		Increased birth mass	1 / 3	Low environmental stochasticity; small mothers benefit most
		Reduced winter mass loss or improved winter condition	5 / 7	Winter forage-limited populations; natural adaptations to winter not compromised (e.g., feeding stations not in thermally unfavorable areas); areas of low human disturbance
		Increased autumn mass or condition	3 / 11	Generally only where supplement provided year round or during summer or autumn; exception may be among yearlings
		Increased offspring autumn mass or condition	4 / 6	Low environmental stochasticity; heavier females benefit most; where additional resources not invested in greater number of offspring
		Increased antler growth	2 / 5	Natural mineral availability is restricted and mineral supplement provided during antler growing season

	Compensation for loss of natural range	Increased carrying capacity	3 / 3	Food-limited populations; adequate water supply; summer forage conditions not limiting
	Improved hunting or viewing opportunities	Increased population size or density	4 / 6	Food-limited populations; harvesting is not limiting
		Increased aggregation or group size	2 / 2	Feeding or baiting during hunting season; medium- to long-term feeding in predictable locations
		Concentration of activity at feeding sites	8 / 8	Feed sites within home range only
		Increased hunting success	1 / 4	Feeding or baiting during hunting season; greater increase in success among archery hunters
Diversionary feeding	Reduced traffic collision rate	Diversion of animals from traffic arteries	1 / 3	Feeding stations at end of migration route or within wintering area
		Restricted ranging (reduced home range size)	3 ^a / 8	Not clear; food-limited populations most likely
		Controlled spatial distribution (altered migration patterns)	3 / 5	Not clear; most likely in areas of little snow, within wintering areas and in combination with fences
	Reduced crop, forest, or habitat damage	Diet changed from crops, trees, or natural forage to provided feed	6 ^b / 16	Where population density is kept low; feed type similar to natural forage; feed sites not near vulnerable vegetation

^a One study showed a significant response in the opposite direction to that intended.

^b Four studies showed a significant response in the opposite direction to that intended.

Table 2. Evidence of the occurrence of unintended effects of feeding wild ungulates in terms of the number of empirical studies providing support per the number of relevant studies. Conditions under which risks of unintended effects are likely to be increased are also given. Full details of all supporting evidence are given in Supplemental Material (Table S3).

Effect on:	Unintended effect	Evidence	Conditions expected to promote risk
Population dynamics	Reduced population fluctuations	0 / 1	Not clear
	Increased population growth rate and reduced density dependence	3 / 3	Food-limited populations before new carrying capacity is approached
Genetics and selection pressures	Changed spatial genetic structure	1 / 1	Where aggregation of multiple kin-structured social groups (e.g., matriline) occurs
	Reduced natural selection	1 / 1	Sufficient feeding to reduce winter mortality but distribution method limits access of subordinates
	Increased variance in male mating success affecting sexual selection	1 / 1	Feeding during rut; polygynous mating systems; aggregation of females; increased female harem size
Behavior	Increased aggression	4 / 5	Restricted access to feed; feed distribution clumped; feed quantity rationed; high animal density
	Increased stress	1 / 1	High density aggregations; high levels of aggression
Vegetation and habitats	Increased local browsing or grazing	4 / 4	Long-term feeding; sustained heavy browsing or grazing; feed distribution clumped
	Increased selective foraging or impact on preferred species	2 / 4	Not clear; may be interannual and seasonal effects; may depend on availability and palatability of alternative forage
	Changed plant species composition	3 / 3	Long-term feeding; sustained heavy browsing or grazing
	Decline in shrubs and woody vegetation or cover	4 / 4	Long-term feeding; sustained heavy browsing or grazing

	Invasion of non-native weed species	2 / 3	Non-local feed; contaminated feed
Other taxa	Negative effect on biodiversity	1 / 3	Sustained heavy browsing or grazing; reduction in habitat or niche heterogeneity; species replacement does not occur
	Impact on non-target species	6 / 7	Large scale, long-term feeding; increased nest predation most likely when feeding during nesting season
Parasite and disease risk	Increased parasitism due to spatial aggregation and increased contact rates	10 / 14	Diseases with density dependent transmission; parasites with direct life cycle; season of transmission coincides with feeding season; feeding within geographic range of infectious disease; few or aggregated feeders; feed delivery facilitates nose-to-nose contact; high pathogen survival in environment; long feeding season
	Reduced parasitism due to improved body condition	2 / 4	Diseases inducing high immunity; food-limited populations
	Feed acts as an effective disease fomite	2 / 2	Feed supports diseases in environment
	Rumen overload	1 / 4	Not clear

SUPPLEMENTAL MATERIAL

Milner, J.M. et al. 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. *Journal of Wildlife Management*.

Types of ungulate feeding

We define supplementary feeding as the intentional provision of additional (normally spatially aggregated) feed, with the aim of enhancing either individual or population size or performance (Ozoga & Verme 1982), including where human development prevents access to part of the annual range (Doenier et al. 1997, Smith 2001, Peterson & Messmer 2011). Feed may be provided year round (Olguin et al. 2013) or during the season of natural food limitation, being the winter at high latitudes (Smith 2001) or the dry season/ summer in Mediterranean environments (Pérez-González et al. 2010, Rodriguez-Hidalgo et al. 2010). Hence, in many areas, supplementary feeding is often called winter feeding. Supplementary feed may occur as a highly organized and repeated, moderate to large scale annual programme as at the National Elk Refuge, Wyoming, U.S.A. (Boyce 1989, Smith 2001) or in the hunting territories, or reviers, of central Europe (Peek et al. 2002, Schmidt 2014). Alternatively feeding may be an *ad hoc* effort to reduce starvation mortality under severe winter conditions (i.e. cold and deep snow), sometimes called emergency provisioning (Baker & Hobbs 1985, Lewis & Rongstad 1998), or recreational feeding by private individuals.

We define diversionary feeding, also known as intercept feeding, as the provision of strategically placed feed aimed at reducing damage to agricultural crops, livestock, timber stands or natural habitats (Geisser & Reyer 2004, Gundersen et al. 2004, Sahlsten et al. 2010, van Beest et al. 2010a). Similarly, it may be used to draw wildlife away from major traffic corridors with the aim of reducing ungulate-vehicle collisions (Wood & Wolfe 1988, Andreassen et al. 2005).

Wildlife baiting involves feeding to attract or hold wildlife in an area (Inslerman et al. 2006). It is often used for the purposes of recreational hunting to attract animals to congregate in specific areas to improve hunting success (Brown & Cooper 2006) or viewing by tourists (Orams 2002), but also for research (e.g. capture wildlife), and the delivery of oral vaccines (e.g. Cross et al. 2007a). Although it is a common practice (both legally and illegally) of large game hunters in many areas (Sorensen & Brook 2011), we limit its inclusion within this review to situations in which its objectives overlap those of supplementary feeding.

Fig. S1. Histograms showing the distribution of studies (total $n = 101$) by (a) location (Europe is all of Europe except Fennoscandia) and feed type (Bulk: pelleted or unprocessed bulk forage crops including silage, hay and other roughage; Concentrates: fruits, root crops, grain or maize (corn) and pelleted concentrates; Both: bulk and concentrates), (b) location and feeding programme history (Short: < 5 y; Medium: 5-20 y; Long: > 20 y), (c) feed type and duration, (d) duration and feed distribution method (Bales; Feed/bait piles; Feeder units & troughs; Spread on ground including feed lines), (e) target species (see Table S4 for Latin names), and (f) location and management goals (S1: improved performance; S2: compensation for loss of range; S3: improved hunting / viewing; D1: reduced collision rate; D2: reduced crop/vegetation damage; D3: restricted ranging, an intended effect of both D1 and D2).

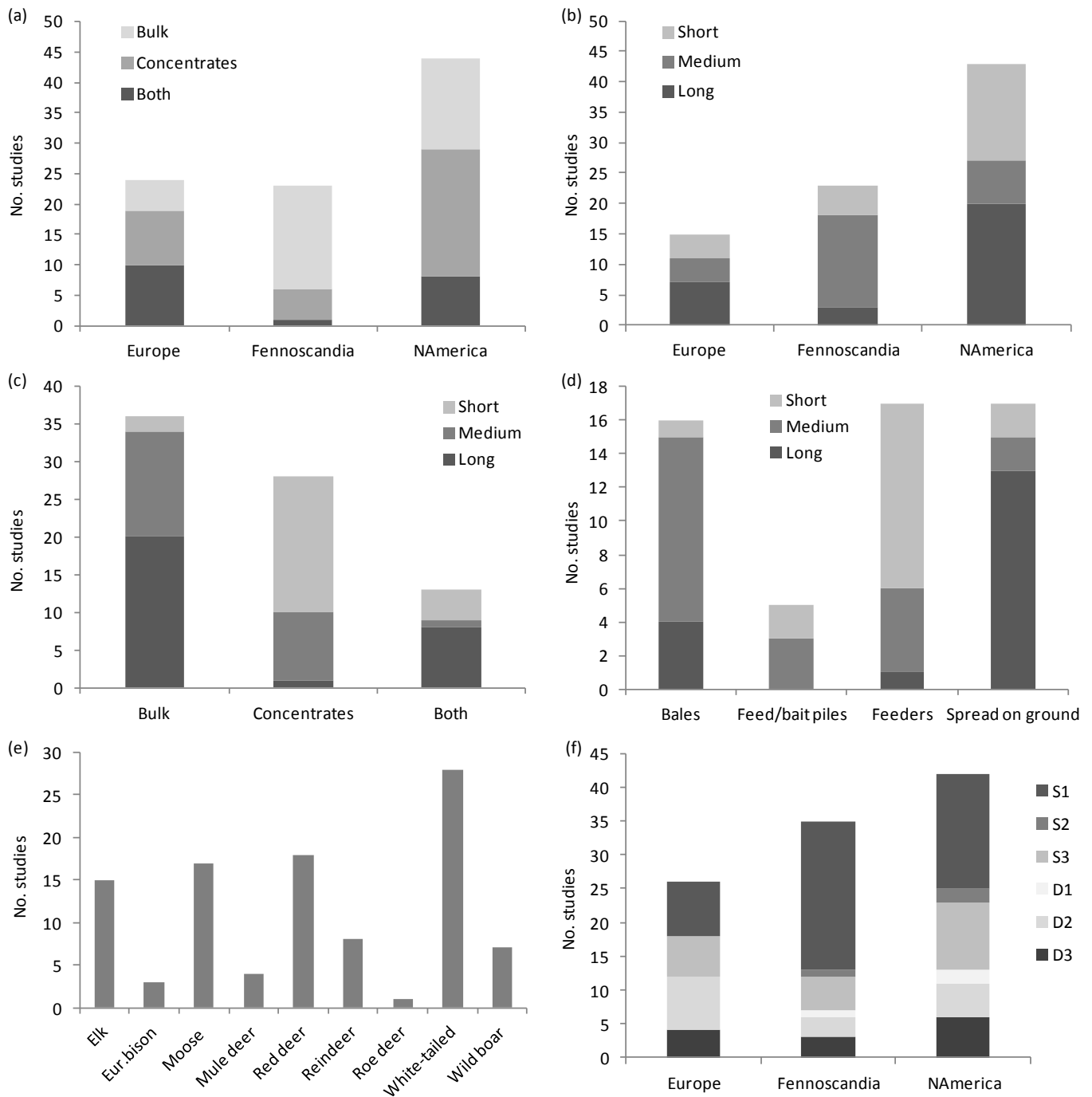


Table S1. Supporting evidence of intended effects of supplementary feeding necessary to meet management goals: a) improving individual or population performance, b) compensating for loss of natural range, c) increasing hunting or viewing opportunities.

Intended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
<i>a) Improving performance</i>										
Increased survival rate	0	Reindeer	N Norway	0 y	Reindeer pellets	n/a	Expt.	F/U	Fauchald et al. 2004	No effect on adult female winter survival (mild winter) or calf summer survival
	0	Reindeer	Finland	0-13 y	Hay	n/a	Obsv.	B/A	Helle & Kojola 1993	
Increased reproductive rate	0	Mule deer	Utah, US	1-5 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2011	Same study area as Peterson & Messmer (2007) but longer-term
	T	Mule deer	Utah, US	1-3 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2007	
	T	Mule deer	Colorado, US	0 y	Commercial ration	n/a	Expt.	F/U	Baker & Hobbs 1985	Emergency feeding in extreme winter
	T	White-tailed deer	Wisconsin, US	0-3 y	Corn & pellets	Feeders	Q-Expt.	F/U	Lewis & Rongstad 1998	Only in severe winter, among fawns
	T	Elk	Wyoming, US	>70 y	Pelleted alfalfa hay	Spread	Obsv.	Amount fed	Smith & Anderson 1998	Calves
	T	Moose	SE Norway	> 20 y	Grass silage	Bales	Q-Expt.	F/U	Milner et al. 2013a	
	T	Reindeer	N Norway	2-10 y	Reindeer pellets	n/a	Q-Expt.	F/U	Ballesteros et al. 2013	
	0	Reindeer	N Norway	3-4 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2008	
	0	Reindeer	N Norway	2 y	Reindeer pellets	n/a	Expt.	F/U	Fauchald et al. 2004	
	T	Mule deer	Utah, US	1-3 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2007	
Increased birth mass	0	Mule deer	Utah, US	1-5 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2011	Same study area as Peterson et al. (2007) but longer-term
	T	White-tailed deer	Michigan, US	1-12 y	Pellets	Feeders	Obsv.	B/A	Ozoga 1987	Fed year round
	T	Red deer	SC Spain	6-20 y	Pellets	Feeders	Q-Expt.	F/U	Rodriguez-Hidalgo et al. 2010	Feeding during summer (limiting season)
Reduced winter mass loss	0	Reindeer	N Norway	0 y	Reindeer pellets	n/a	Expt.	F/U	Fauchald et al. 2004	
	T	Reindeer	N Finland	> 13 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2009	
	0	Elk	Wyoming, US	>70 y	Pelleted alfalfa hay	Spread	Obsv.	Amount fed	Smith 1998	
	T	Moose	S, SE Norway	5-20 y	Grass silage	Bales	Q-Expt.	F/U	Milner et al. 2013a, van Beest & Milner 2013	Adult females & calves

Continued...

Intended effect	Evidence¹	Species²	Locality	Feeding history³	Feed type³	Distrib. method⁴	Study design⁵	Comparisons⁶	Reference	Notes
Reduced winter mass loss/ increased winter mass / condition	T	Reindeer	N Norway	2 y	Reindeer pellets	n/a	Expt.	F/U	Fauchald et al. 2004	
	T	Reindeer	N Finland	> 13 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2009	Also lagged effect in small adult females
	0	Reindeer	N Finland	n/a	Concentrates & silage	Feeders	Expt.	F/U	Holand et al. 2012	
	0	Mule deer	Utah, US	1-3 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2007	12% high body condition indices in fed deer but not significant ($p=0.052$)
	T	White-tailed deer	Michigan, US	1-12 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982, Timmons et al. 2010	All age-sex classes; fed year round
Increased autumn / early winter body mass / condition	T	White-tailed deer	Texas, US	2-3 y	Pelleted concentrate	Feeders	Expt.	F/U & density	Timmons et al. 2010	Fed year round
	0	Moose	S, SE Norway	5-20 y	Grass silage	Bales	Q-Expt.	F/U	van Beest & Milner 2013	Adult females
	0	Reindeer	N Norway	2-10 y	Reindeer pellets	n/a	Q-Expt.	F/U	Ballesteros et al. 2013	Adult females
	0	Reindeer	N Norway	3-4 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2008	Also no effect on adult female mass after parturition (Fauchald et al. 2004)
	E	Reindeer	N Finland	0-20 y	Dried hay	n/a	Q-Expt.	Feeding gradient	Helle & Kojola 1994	Adult females in one study area only
	0	Reindeer	N Finland	> 13 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2009	
	E	White-tailed deer	Texas, US	> 5 y	Pellets	Feeders	Q-Expt.	F/U	Bartoskewitz et al. 2003	Effect of summer feeding in males & 2.5 y-old females only & effect of autumn/early winter feeding on male mass in current year
	T	White-tailed deer	Texas, US	2-3 y	Pelleted concentrate	Feeders	Expt.	F/U & density	Timmons et al. 2010	Fed year round
	T	Red deer	Spain	3 y	Pellets	Feeders	Expt.	F/U	Olguin et al. 2013	Fed year round. Small effect on live mass & kidney fat index, no effect on carcass mass or size
	0	Red deer	Slovenia	1-60 y	Hay, silage or maize	n/a	Obsv.	Feeding gradient	Jerina 2007	
	T	Red deer	SC Spain	6-20 y	Pellets	Feeders	Q-Expt.	F/U	Rodriguez-Hidalgo et al. 2010	Fed during summer (limiting season)
0	Red deer, wild boar	Netherlands	n/a (long term)	Maize, mineral lick, etc	n/a	Obsv.	B/A	Groot Bruinderink et al. 2000	No effect of cessation of feeding (but density also reduced)	

Continued...

Intended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes	
Increased offspring autumn / early winter mass	T	Reindeer	N Norway	0 y	Protein/mineral supplement	n/a	Expt.	F/U	Jacobsen et al. 1981	Increased milk production, no effect on milk composition	
	T	Reindeer	N Finland	0-20 y	Dried hay	n/a	Q-Expt.	Feed gradient	Helle & Kojola 1994		
	T	Reindeer	N Norway	2-10 y	Reindeer pellets	n/a	Q-Expt.	F/U	Ballesteros et al. 2013		
	T	Reindeer	N Norway	3-4 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2008		
Increased antler growth										Effect stronger in females with higher body mass & only for long-term feeding / low environmental stochasticity	
	0	Reindeer	N Finland	> 13 y	Reindeer pellets	n/a	Expt.	F/U	Bårdsen et al. 2009		
	0	Moose	S & SE Norway	5-20 y	Grass silage	Bales	Q-Expt.	F/U	Milner et al. 2012		
	0	Red deer	Netherlands	n/a (long term)	Maize, mineral lick, etc	n/a	Obsv.	B/A	Groot Bruinderink et al. 2000		No effect of cessation of feeding (but density also reduced)
	T	Red deer	Spain	n/a	Grain, pellets, straw, mineral blocks	n/a	Obsv.	F/U	Landete-Castillejos et al. 2013		Low density improved antler structure but did not compensate for mineral deficiencies
	0	Elk	Wyoming, US	>70 y	Pelleted alfalfa hay	Spread	Obsv.	Amount fed	Smith 1998		No effect of feeding on size of antlers in males that died the following winter
	T	White-tailed deer	Michigan, US	1-12 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982		All antler measures increased except beam diameter of 2.5 y olds & no. points of 1.5 y olds
E	White-tailed deer	Texas, US	> 5 y	Pellets	Feeders	Q-Expt.	F/U	Bartoskewitz et al. 2003	Effect of summer feeding on 1 of 2 ranches, and only in 3.5 y-old males		
<i>b) compensating for loss of natural range</i>											
Increased carrying capacity	T	Elk	Wyoming, US	> 100 y	Pelleted or baled hay	Bales, spread	Obsv.	None	Smith 2001		
	T	Reindeer	N Norway	2-10 y	Reindeer pellets	n/a	Q-Expt.	F/U	Ballesteros et al. 2013		
	T	White-tailed deer	Michigan, US	1-12 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982	Carrying capacity increased to peak & then declined at highest density	

Continued...

Intended effect	Evidence¹	Species²	Locality	Feeding history³	Feed type³	Distrib. method⁴	Study design⁵	Comparisons⁶	Reference	Notes
<i>c) Increasing hunting or viewing opportunities</i>										
Increased population size or density	T	Reindeer	N Norway	2-10 y	Reindeer pellets	n/a	Q-Expt.	F/U	Ballesteros et al. 2013	
	T	Red deer	SC Spain	6-20 y	Pellets	Feeders	Q-Expt.	F/U	Rodriguez-Hidalgo et al. 2010	Feeding during summer (limiting season)
	0	Red deer	W Spain	n/a	Maize, alfalfa pellets, silage	n/a	Q-Expt.	F/U	Pérez-González et al. 2010	Females only; tendency towards higher density
	0	Mule deer	Utah, US	1-5 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2011	
	T	Moose	SE Norway	> 20 y	Grass silage	Bales	Q-Expt.	Over time	Milner et al. 2012	Density kept constant despite decline in natural forage
Increased aggregation	T	White-tailed deer	Michigan, US	1-12 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982	
	T	Red deer	Spain	< 1 y	Alfalfa pellets	Spread	Expt.	B/T1/T2	Sánchez-Prieto et al. 2004	
Concentration of activity at feeding sites	T	Red deer	W Spain	n/a	Maize, alfalfa pellets, silage	n/a	Q-Expt.	F/U	Pérez-González et al. 2010	Females only; increased aggregation & harem size
	T	Moose	N Sweden	1 y	Grass silage	Bales	Q-Expt.	B/A	Sahlsten et al. 2010	
	T	Moose	SE Norway	> 20 y	Grass silage	Bales	Obsv.	T/C	Gundersen et al. 2004	
	T	Moose	S Norway	c. 6 y	Grass silage	Bales	Obsv.	F/U	van Beest et al. 2010 <i>b</i>	
	T	White-tailed deer	Connecticut, US	< 1 y	n/a (bait)	Piles	Obsv.	B/A	Kilpatrick & Stober 2002	No effect on core area size but shift in location if bait site within home range
	T	White-tailed deer	Texas, US	0-1 y	Shelled corn	Feeders	Expt.	F/U	Cooper et al. 2006	Females reduced 50% core area
	T	White-tailed deer	Wisconsin, US	< 2 y	Shelled corn	n/a	Expt.	F1/F2/U	Thompson et al. 2008	Feed use increased & intensity greater at rationed piles than ad lib. spreads
	T	Red deer	Slovenia	1-60 y	Hay, silage or maize	n/a	Obsv.	Feeding gradient	Adamič & Jerina 2010	
	T	European bison	Białowieża, Poland	> 50 y	Grass silage, hay	Bales	Q-Expt.	F1/F2/U	Radwan et al. 2010	
Increased hunting success	0	White-tailed deer	Michigan, US	> 6 y	n/a (bait)	Piles	Q-Expt.	F/U	Rudolph et al. 2006	

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Intended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
Increased hunting success	T	White-tailed deer	Connecticut, US	n/a	n/a (bait)	n/a	Obsv.	F/U	Kilpatrick et al. 2010	Increased success among bow hunters
	0	White-tailed deer	Pennsylvania, US	1-3 y	Corn	Piles	Obsv.	F/U	Tardiff Fleegle & Rosenberry 2010	
	E	White-tailed deer	Wisconsin, US	n/a	n/a (bait)	n/a	Q-Expt.	F/U	van Deelen et al. 2006	Increase in archery harvest offset by decrease in firearm harvest

¹ T - hypothesis is supported; F - hypothesis not supported & opposite trend shown; 0 - no evidence of effect; E – evidence equivocal.

² Species Latin names given in Table S4.

³ n/a – information not available

⁴ Feed distribution method: Bales – forage presented in bales; Feeders – barrel , elevated & gravity-fed units, troughs, etc; Spread – feed spread on ground including in feed lines; Piles – feed/ bait heaped on ground in clumped piles; n/a - information not available

⁵ Expt. – experiment; Q-Expt. – quasi experiment (treatment/control design based on variation within / between populations); Obsv. – observational study.

⁶ F/U - fed / unfed; B/A - before / after; T/C - treatment / control; B/T1/T2- before, treatment 1/ treatment 2; F1/F2/U- high intensity or ad lib. feeding / low intensity or rationed feeding /no feeding; Density & Feed – density & feeding intensity gradient.

Table S2. Supporting evidence of intended effects of diversionary feeding necessary to meet management goals: a) reducing vehicle collisions, b) reducing damage to crops, forestry, and natural habitats. (¹⁻⁶ See footnotes to Table S1)

Intended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
<i>a) Reducing vehicle collisions</i>										
Diversion of animals from traffic arteries	T	Moose	SE Norway	0-10 y	Grass silage	Bales	Q-Expt.	T/C	Andreassen et al. 2005	
	O	Mule deer	Utah, US	0-4 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2011	
	O	Mule deer	Utah, US	0-1 y	Alfalfa hay, pellets, apples	n/a	Expt.	T/C	Wood & Wolfe 1988	Treatments only reduced no. collisions significantly in 2/6 trials
Restricted ranging (reduced home range size)	F	White-tailed deer	Texas, US	> 4y	Pelleted protein feed	Feeders	Obsv.	F/U	Webb et al. 2008	Adult males
	O	White-tailed deer	Texas, US	< 2 y	Shelled corn	Feeders	Expt.	F/U	Cooper et al. 2006	
	O	White-tailed deer	Québec, Canada	< 2 y	Grain & high energy pellets	Feeders	Expt.	F/U	Grenier et al. 1999	
	O	White-tailed deer	Connecticut, US	< 1 y	n/a (bait)	Piles	Obsv.	B/A	Kilpatrick & Stober 2002	Females only - activity centres affected
	T	Red deer	Slovenia	1-60 y	Hay, silage or maize	Feeders	Obsv.	Feeding gradient	Jerina 2012	
	T	Red deer	Austria	n/a	Hay, turnips, maize & grain	Spread, feeders	Obsv.	F/U	Schmidt 1993	Not tested statistically
	T	Red deer	Germany	n/a	Hay, silage	n/a	Obsv.	F/U	Reinecke et al. 2014	
	O	Moose	S Norway	c. 6 y	Grass silage	Bales	Obsv.	F/U	van Beest et al. 2011	
Controlled spatial distribution (altered migration patterns)	O	Moose	N Sweden	1 y	Grass silage	Bales	Q-Expt.	B/A	Sahlsten et al. 2010	No effect on probability of migration, migration distance or route
	T	Red deer	N Italy	n/a	n/a	n/a	Obsv.	F/U	Luccarini et al. 2006	Migrants more closely associated with feed sites in winter than residents
	O	Moose	S & SE Norway	5-20 y	grass silage	Bales	Q-Expt.	F/U	Milner et al. 2012	Migration strategy independent of feed use
	T	Mule deer	Utah, US	1-3 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2007	Probability of migration unchanged but fed deer migrated later in spring
	T	White-tailed deer	Wisconsin, US	0-3 y	Corn & pellets	Feeders	Q-Expt.	F/U	Lewis & Rongstad 1998	Reduced probability of migration in winter-fed deer; no effect on timing of spring migration

Continued...

Intended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
<i>b) Reducing crop, forestry & habitat damage</i>										
Diet changed from crops, trees or natural forage to provided feed	T	European bison	Białowieża, Poland	> 50 y	Grass silage, hay	Bales	Q-Expt.	F/U	Kowalczyk et al. 2011	Feeding reduces foraging on winter crops
	F	Moose	SE Norway	> 20 y	Grass silage	Bales	Q-Expt.	Spatial & temporal	Gundersen et al. 2004, van Beest et al. 2010a, Mathisen et al. 2014	
	O	Moose	S Norway	5-6 y	Grass silage	Bales	Q-Expt.	F/U	van Beest et al. 2010b	No difference in selection for vulnerable forest stands
	O	Moose	Finland	0-2 y	Aspen & pine tops	Treetops	Expt.	T/C	Lääperi 1990	Increased use of treatment sites & partial reduction in damage
	T	Red deer	Slovakia	< 1y	Hay, silage & pellets	Feeders	Expt.	T/C	Rajský et al. 2008	Provision of concentrates reduced bark stripping
	O	Red deer	Europe	n/a	n/a	n/a	Q-Expt.	T/C	Verheyden et al. 2006	Bark stripping
	F	Wild boar	NE Poland	n/a	Maize plants	Planted*	Obsv.	Spatial & temporal	Frackowiak et al. 2013	*Protective field strips of maize
	O	Wild boar	SE France	< 1 y	Maize grain	Spread	Expt.	B/A	Calenge et al. 2004	Damage reduction not significant. Compensation paid reduced by 60%
	T	Wild boar	Karelia	n/a	Corn & Hay	n/a	Expt.	B/A	Belkin et al. 2012	
	O	Wild boar	Thurgau, Switzerland	c. 4-6 y	Fruits, maize, potatoes & pellets	Piles	Obsv.	Temporal	Geisser & Reyer 2004	
	T	European bison	Białowieża, Poland	> 50 y	Grass silage, hay	Bales	Q-Expt.	F/U	Kowalczyk et al. 2011	Reduced proportion of woody browse in diet. Preferred browse sp. were not commercially important
	O	Elk	Wyoming, US	> 100 y	Baled hay / pelleted alfalfa	Bales, spread	Obsv.	Spatial	Smith et al. 2004	
	T	White-tailed deer	Texas, US	2-3 y	Pelleted concentrate	Feeders	Expt.	F/U & density	Timmons et al. 2010	Fed year-round. Reduced proportion of mast eaten in fall & increased proportion of browse in spring
	T	White-tailed deer	Ontario, Canada	0 y	Corn & oats	Feeders	Expt.	F/U	Schmitz 1990	Browse consumption reduced (not tested statistically) but greater than expected
	F	White-tailed deer	Minnesota, US	0-1 y	Commercial pellets	Feeders	Q-Expt.	F/U	Doenier et al. 1997	
	F	White-tailed deer	Texas, US	1	Corn	Feeders	Expt.	F/U	Cooper et al. 2006	Both sexes

Table S3. Supporting evidence for the occurrence of potential unintended effects of feeding wild ungulates

Effect on:	Unintended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
Population dynamics	Reduced density dependence	T	Elk	Wyoming, US	> 70 y	alfalfa pellets	Spread	Mod.	None	Smith & Anderson 1998, Lubow & Smith 2004	
	Increased pop growth rate	T	Reindeer	N Norway	2-10 y	reindeer pellets	n/a	Q-Expt.	F/U	Ballesteros et al. 2013	
		T	White-tailed deer	Michigan, US	1-12 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982	Not tested statistically
		T	Reindeer	N Norway	2-10 y	reindeer pellets	n/a	Q-Expt	F/U	Ballesteros et al. 2013	
Genetics & selection pressures	Changed spatial genetic structure	T	White-tailed deer	Michigan, US	> 20 y	Grain, vegetables, fruits, feed plots, forage crops	n/a	Q-Expt.	B/A	Blanchong et al. 2006	Comparison during last year of feeding & 2 nd year after feeding ban
	Reduced intercohort variation (improved condition)	T	Red deer	Austria	> 30 y	Hay, maize silage, turnip	Spread, feeders	Q-Expt.	F/U (with literature*)	Schmidt & Hoi 2002	* Not tested statistically
	Reduced intracohort variation (improved condition)	F	Red deer	Austria	> 30 y	Hay, maize silage, turnip	Spread, feeders	Q-Expt.	F/U (with literature*)	Schmidt & Hoi 2002	* Not tested statistically
	Increased intra-cohort variation (reduced natural selection)	T	Red deer	Austria	> 30 y	Hay, maize silage, turnip	Spread, feeders	Q-Expt.	F/U (with literature*)	Schmidt & Hoi 2002	* Not tested statistically
	Increased variance in male mating success affecting sexual selection	T	Red deer	Spain	< 1 y	Alfalfa pellets	Spread	Expt.	B/T1/T2	Sánchez-Prieto et al. 2004	Females only; feeding treatments clumped vs. dispersed; feeding increased F harem size
Behavior	Increased aggression	T	Red deer	W Norway	n/a	Hay	Spread	Obsv.	with literature*	Veiberg et al. 2004	*Not tested statistically
		T	Red deer	Spain	n/a	Alfalfa pellets	Spread	Expt.	B/T1/T2	Sánchez-Prieto et al. 2004	Increased M-M aggression & M-F harassment, reduced harassment per F due to F aggregation
		T	Red deer	W Spain	n/a	Maize, alfalfa pellets, silage	n/a	Q-Expt.	F/U	Pérez-González et al. 2010	Females only
		T	Elk	Yellowstone, US	> 100 y	Grass or alfalfa hay	Spread	Obsv.	B/A	Forristal et al. 2012	Aggression rates much greater during than before feeding
		0	White-tailed deer	Wisconsin, US	< 2y	Shelled corn	Piles, spread	Expt.	F1/F2/U	Thompson et al. 2008	No difference in either agonistic or close contact behaviours

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Effect on:	Unintended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
	Increased stress	T	elk	Yellowstone, US	> 100 y	Grass or alfalfa hay	Spread	Expt.	B/A-T/C	Forristal et al. 2012	Stress response strongly correlated with elk density
Habitat & vegetation	Increased local browsing / grazing	T	Moose	SE Norway	10-20 y	Grass silage	Bales	Q-Expt.	T/C	Gundersen et al. 2004, van Beest et al. 2010a	
		T	White-tailed deer	Minnesota, US	0-1 y	Commercial pellets	Feeders	Q-Expt.	F/U	Doenier et al. 1997	Browsing similar within 100 m of feed & control sites, higher in area to 900 m of feed sites
		T	White-tailed deer	Texas, US	< 2 y	Shelled corn	Feeders	Expt.	F/U	Cooper et al. 2006	
		T	Elk	Wyoming, USA	60-90 y	Hay / pelleted alfalfa	Spread	Q-Expt.	F/U	Anderson 2007	
	Increased selective foraging / impact on preferred species	O	White-tailed deer	Texas, US	0 y	Pellets	n/a	Expt.	F/U	Murden & Risenhoover 1993	Strong but non-significant trend (small sample size)
		E	White-tailed deer	Texas, US	2-3 y	Pelleted concentrate	Feeders	Expt.	F/U & density	Timmons et al. 2010	Fed year-round. Feeding only increased selectivity in autumn
		T	Mule deer	Utah, US	1-5 y	Corn, alfalfa hay & pellets	Feeders	Expt.	F/U	Peterson & Messmer 2011	Effect on utilisation of preferred but not less preferred sp.
	Changed plant species composition	T	White-tailed deer	Michigan, US	5 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982	Decline in preferred species
		T	Elk	Wyoming, US	25 y	Alfalfa/ grass hay	Spread	Q-Expt.	B/A-T/C	Rinella et al. 2012	
		T	Moose	SE Norway	20 y	Grass silage	Bales	Q-Expt.	Spatial	Pedersen et al. 2014	Shift from dwarf-shrub to grass & herb dominated field layer
Decline in shrubs & woody vegetation / cover	T	White-tailed deer	Michigan, US	5 y	Pellets	Feeders	Obsv.	B/A	Ozoga & Verme 1982	Decline in preferred species	
	T	Elk	Yellowstone, US	> 100 y	Baled hay / pelleted alfalfa	Bales, spread	Obsv.	Temporal	Smith et al. 2004	Local scale decline only	
	T	Elk	Wyoming, US	25 y	Alfalfa/ grass hay	Spread	Q-Expt.	B/A-T/C	Rinella et al. 2012		
	T	Elk	Wyoming, USA	60-90 y	Hay / pelleted alfalfa	Spread	Q-Expt.	F/U	Anderson 2007		
		T	Moose	SE Norway	10-20 y	Grass silage	Bales	Q-Expt.	T/C	Pedersen et al. 2007, Pedersen et al. 2014	

<i>Continued</i>											
Effect on:	Unintended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
Habitat & vegetation	Invasion of non-native species	T	Elk	Wyoming, US	25 y	Alfalfa/ grass hay	Spread	Q-Expt.	B/A-T/C	Rinella et al. 2012	Invasion by smooth brome
		T	Elk	Yellowstone, US	> 100 y	Baled hay / pelleted alfalfa	Bales, spread	Obsv.	None	Smith et al. 2004	
		0	European bison	Białowieża, Poland	> 50 y	Grass silage, hay	Bales	Q-Expt.	F/U	Jaroszewicz et al. 2009	Difference in no. seedlings & no. sp./ dung sample not significant between fed & wild groups
Other taxa	Negative effect on biodiversity	0	Moose	SE Norway	> 16 y	Grass silage	Bales	Q-Expt.	T/C	Mathisen & Skarpe 2011	Zero net impact on passerine abundance & diversity: positive & negative effects balanced
		0	White-tailed deer	Texas, US	4-5 y	Pelleted concentrates	Feeders	Expt.	F/U & density	Moseley et al. 2011	No impact on species richness of rodent community
		T	Elk	Wyoming, US	60-90 y	Hay / pelleted alfalfa	Spread	Q-Expt.	F/U	Anderson 2007	Reduced abundance & diversity of birds, shift in composition.
	Impacts on non-target species	T	Moose	SE Norway	> 12 y	Grass silage	Bales	Q-Expt.	T/C	Mathisen et al. 2012	Direction of effect on passerines depends on diet
		T	Moose	SE Norway	10-12 y	Grass silage	Bales	Q-Expt.	T/C	Pedersen et al. 2007	Reduced breeding success of <i>Parus major</i>
		T	White-tailed deer	Texas, US	< 4 y	Shelled corn	Feeders	Expt.	F/U	Cooper & Ginnett 2000	Increased turkey nest predation in non-drought years
		T	White-tailed deer	Florida, US	n/a	Corn	Feeders	Expt.	F/U	Hamilton et al. 2002	Increased freshwater turtle nest predation
		T	Ungulate game sp.	Carpathians, Poland	Many years	Maize, beetroots, fodder, grain	Spread	Expt.	T/C	Selva et al. 2014	Increased predation of artificial nests
		T	Moose	SE Norway	18-20 y	Grass silage	Bales	Q-Expt.	T/C	Pedersen et al. 2014	Increased abundance of shrews & <i>Myocrotus</i> voles, decreased abundance of bank voles, total biomass unaffected
		0	White-tailed deer	Texas, US	4-5 y	Pelleted concentrates	Feeders	Expt.	F/U & density	Moseley et al. 2011	No impact on rodent populations
Disease & parasite risk	Increased transmission due to aggregation	T	White-tailed deer	Michigan, US	> 5 y	n/a	Piles	Obsv.	Feed	Hickling 2002	Prevalence of bovine TB correlated with deer density & feeding/baiting

Continued..

Effect on:	Unintended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
Disease & parasite risk	Increased transmission due to aggregation & increased contact rates	T	White-tailed deer	Michigan, US	> 20 y	Grain, vegetables, fruits, feed plots, forage crops	n/a	Obsv.	Density & Feed	Miller et al. 2003	Prevalence of bovine TB increased with feeding
		T	Red deer	SC Spain	n/a	Grain or pellets	Feeder, spread	Q-Expt.	F/U	Vicente et al. 2007a, Vicente et al. 2007b	Prevalence of bovine TB increased with density (high at sites with feeding) & with aggregation of wild boar at feeder units
		0	Red deer	SC Spain	n/a	Grain or pellets	Feeder, spread	Q-Expt.	F/U	Vicente et al. 2007a	Pulmonary nematodes unaffected by host density
		T	Red deer	SW Spain	n/a	n/a	Spread	Q-Expt.	F/U	Castillo et al. 2011	Increased prevalence of bovine TB
		T	Elk	Yellowstone, US	> 100 y	Hay	Spread	Obsv.	F/U	Bienen & Tabor 2006, Cross et al. 2007b, 2010a, 2010b	Increased brucellosis prevalence
		T	Elk	Idaho, US	long	n/a	Spread	Obsv.	F/U*	Etter & Drew 2006	Increased brucellosis prevalence. *Not tested statistically
		T	Elk	Yellowstone, US	> 100 y	Hay / pelletd alfalfa	Spread	Expt.	F1 / F2	Creech et al. 2012	Low density feeding resulted in 70% decrease in foetal contact rate
		T	Elk	Yellowstone, US	> 100 y	Hay/ alfalfa pellets	Spread	Q-Expt.	F/U	Hines et al. 2007	Increased exposure to GI parasites
		0	Moose	SE Norway	> 20 y	Grass silage	Bales	Q-Expt.	F/U	Milner et al. 2013b	GI nematodes
		T	European bison	Białowieża, Poland	> 50 y	Grass silage, hay	Bales	Q-Expt.	F/U	Radwan et al. 2010	Increased intensity of infection with blood-sucking nematode
		T	Wild boar	SW Spain	n/a	Maize	Feeders	Obsv.	Density & Feed	Navarro-Gonzalez et al. 2013	Feeder density more important than host density for gastrointestinal parasites
		0	Wild boar	SC Spain	n/a	Grain or pellets	Feeder, spread	Q-Expt.	F/U	Vicente et al. 2007b	Prevalence of bovine TB associated with aggregation at artificial watering holes but not feeders
		0	Wild boar	SW Spain	n/a	Maize	Feeders	Obsv.	Density & Feed	Navarro-Gonzalez et al. 2013	Pulmonary parasitism influenced by host age & sex but unaffected by host density or feeding intensity

Continued..

Effect on:	Unintended effect	Evidence ¹	Species ²	Locality	Feeding history ³	Feed type ³	Distrib. method ⁴	Study design ⁵	Comparisons ⁶	Reference	Notes
Disease & parasite risk	Reduced parasitism due to improved body condition	T	Red deer	SC Spain	n/a	Grain or pellets	Feeder, spread	Q-Expt.	F/U	Vicente et al. 2007a	Reduced abundance of pulmonary nematodes with increasing condition
		O	Red deer	SC Spain	n/a	Grain or pellets	Feeder, spread	Q-Expt.	F/U	Vicente et al. 2007a	Bovine TB unrelated to individual body condition
		T	Elk	Yellowstone, US	> 100 y	Hay/ alfalfa pellets	Spread	Q-Expt.	F/U	Hines et al. 2007	Decreased susceptibility to GI parasites among fed elk
Disease & parasite risk	Feed acts as a disease fomite	O	Moose	SE Norway	> 20 y	Grass silage	Bales	Q-Expt.	F/U	Milner et al. 2013b	GI nematodes - no detectable effect
		T	n/a	Michigan, USA	> 20 y	Apples, corn, carrots, beets, potatoes, hay	n/a	Q-Expt.	none	Palmer & Whipple 2006	Bovine TB survives on feed up to 112 days at -20C
		T	n/a	Michigan, USA	> 20 y	Corn, hay	n/a	Q-Expt.	none	Fine 2006	Bovine TB viable on feed for up to 58 days
		E	Moose	North Dakota, US	> 20 y	Corn in agricultural fields	Spread	Obsv.	none	Butler et al. 2008	Results not conclusive, difficult to prove as cause of death
		E	Roe deer	Austria	n/a	Fruits, grains, seeds, beet	Piles	Obsv.	none	Ritz et al. 2013	
Rumen overload		T	White-tailed deer	Saskatchewan, Canada	n/a	Grain	n/a	Obsv.	with/ without grain in rumen	Wobeser & Runge 1975	Eating excessive quantities of feeds high in carbohydrate cause of mortality in some individuals
		E	White-tailed deer	Pennsylvania US	n/a	Grain	n/a	Obsv.	none	Woolf & Kradel 1977	

¹⁻⁶See footnotes to Table S1

Table S4. Latin names of species occurring in the reviewed papers ($n = 101$).

Common name	Latin name	No. studies
Elk or Wapiti	<i>Cervus canadensis, Cervus elaphus</i>	15
European bison	<i>Bison bonasus</i>	3
Moose or European elk	<i>Alces alces</i>	17
Mule deer	<i>Odocoileus hemionus</i>	4
Red deer	<i>Cervus elaphus</i>	18
Reindeer	<i>Rangifer tarandus</i>	8
Roe deer	<i>Capreolus capreolus</i>	1
White-tailed deer	<i>Odocoileus virginianus</i>	28
Wild boar	<i>Sus scrofa</i>	7

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