

1 Ergon, T., R. Ergon, M. Begon, S. Telfer, and X. Lambin. 2011. Delayed density-
2 dependent onset of spring reproduction in a fluctuating population of field voles.
3 *Oikos* **120**:934-940.
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5 Delayed density-dependent onset of spring reproduction in a fluctuating
6 population of field voles
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24 Running head: delayed density dependent reproduction

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26 Article paper for *Oikos*. 24 pages including one appendix for *Oikos*' homepage (Matlab code)

27

28 ABSTRACT

29 Delayed density-dependent demographic processes are thought to be the basis for multi-annual
30 cyclic fluctuations in small rodent populations, but evidence for delayed density dependence of
31 a particular demographic trait is rare. Here, using capture-recapture data from 22 sites collected
32 over nine years, we demonstrate a strong effect of population density with a one-year lag on
33 the timing of the onset of spring reproduction in a cyclically fluctuating population of field
34 voles (*Microtus agrestis*, L.) in northern England. The mean date for the onset of spring
35 reproduction was delayed by about 24 days for every additional 100 voles/ha in the previous
36 spring. This delayed density dependence is sufficient to generate the type of cyclic population
37 dynamics described in the study system.

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39 Key words: delayed density dependence, population cycles, demography, capture recapture,
40 lag, vole, seasonality

41

42

43 INTRODUCTION

44 It is now generally accepted that population regulation can only be due to mechanistic links
45 between present and/or past population densities and per capita population growth (Murdoch
46 1994; Turchin 1995). Nevertheless, such density dependence may not be easy to detect. First,
47 population growth may be held back most of the time by density independent processes so that
48 populations only occasionally reach densities where density dependent factors are strong
49 enough to be detected (Turchin 1995). Second, density dependent mechanisms may act with a
50 time-delay and may thus be less obvious (Murdoch 1994; Berryman 2002b; Turchin 2003).

51 The long term dynamics of a population can be viewed as a stochastic process affected
52 by direct and delayed density dependence together with density independent environmental
53 effects (Royama 1992; Stenseth 1999). When delayed density dependent negative feedback is
54 sufficiently strong and with a long enough time-lag, the population dynamics may in certain
55 circumstances be inherently cyclic (Berryman 2002b; Turchin 2003). Indeed, most evidence of
56 delayed density dependence comes from studies of cyclic populations of vertebrates and insects
57 (Berryman 2002a). Further, it has been argued that delayed density dependence in cyclic
58 populations is generally caused by trophic interactions rather than intrinsic mechanisms in the
59 population (Berryman 2002a; Turchin 2003).

60 Different ecological processes are expected to affect different demographic traits, and
61 these effects may be season and age specific. Thus, the demographic syndrome observed in a
62 fluctuating population is more informative with respect to the underlying ecological process
63 than changes in population size (Oli and Dobson 2001; Dobson and Oli 2001; Clutton-Brock
64 and Coulson 2002; Benton *et al.* 2006). Indeed, widely different ecological processes may
65 result in identical or similar density dependent structure and emerging dynamics at the
66 population level (McCauley and Murdoch 1987; Lambin *et al.* 2002).

67 Several analyses of small rodent time-series of spring- and autumn abundance data have
68 concluded that delayed density dependence acting on the populations from autumn to spring is

69 an indispensable feature of the population cycles in the studied systems (Stenseth 1999;
70 Stenseth *et al.* 2003; Bierman *et al.* 2006; Saitoh *et al.* 2006). In northern latitude areas where
71 reproduction often starts long before snowmelt, spring abundance data are often obtained after
72 the onset of the reproductive season. Thus, apparent delayed density dependence during the
73 winter season may reflect effects on either winter survival and/or reproduction in the spring.

74
75 In this study, by contrast, we focus explicitly on the timing of reproductive
76 commencement after the winter. Although this is a demographic trait that shows particularly
77 large variation amongst overwintering cohorts in cyclic populations (Krebs and Myers 1974;
78 Ergon *et al.* 2009), and in which delayed density dependence is sufficient to generate multi-
79 annual population cycles in small rodents (Smith *et al.* 2006), the empirical density dependent
80 structure of the variation in this trait has not previously been well described. Here we use
81 capture-mark-recapture data from cyclic populations of field voles (*Microtus agrestis*, L.) in
82 Kielder Forest, Northern England, we estimated the date that 50 % of females had given birth
83 for their first time during spring, and partitioned the variation in onset of spring reproduction
84 into density dependent and density independent components as well as measurement error. We
85 can thus evaluate the importance of delayed density dependence of this demographic
86 component for generating multi-annual population fluctuations. Although we do not directly
87 address the specific mechanisms behind the variation in onset of spring reproduction, we
88 discuss the potential relevance of various hypothesized mechanisms in the study system.

90 METHODS

92 *Study system and data*

93 Kielder Forest is a large spruce plantations (>600 km²) on the border between England and
94 Scotland. Field voles (*Microtus agrestis*, L.), by far the most numerous small rodents in the

95 area, are confined to distinct grass covered clear-cuts enclosed by dense tree stands that are
96 uninhabitable for voles because they lack ground vegetation. Field voles are microtine rodents
97 (Subfamily Arvicolinae) relying primarily on grasses as forage. Female field voles in the spring
98 may give birth repeatedly at about 20 days interval under good conditions (Ergon et al. 2001b),
99 and offspring born in spring may conceive their first litter immediately after weaning (at 2-3
100 weeks of age). Survival rates are generally low and very few individuals live as long as a year
101 in the field (Graham and Lambin 2002). Field vole sub-populations in Kielder forest fluctuate
102 somewhat asynchronously but nevertheless with a characteristic period of 3 - 5 years (Lambin
103 *et al.* 2000; Bierman *et al.* 2006), making the area particularly well suited for replicated studies
104 on the direct and delayed density dependence of demographic traits. Studies of wintering voles
105 and the onset of spring reproduction are also made easy by the absence of permanent snow
106 cover during winter (detailed description of the study system in (Lambin *et al.* 2000; Graham
107 and Lambin 2002). Green vegetation in winter is overwhelmingly dominated by the semi
108 perennial grass *Deschampsia caespitosa* and by *Juncus effusus*.

109 We made use of capture-recapture data of field voles collected over a period of nine
110 years (1996 to 2004) from 22 different forest clear-cuts (sites) in Kielder Forest. The data from
111 each site covered one to six years, giving 47 datasets defined by a unique site and year. Each
112 dataset consisted of individual capture records taken from one to six primary trapping sessions
113 (separated by two to four weeks) that took place before the capture of the first juveniles in the
114 spring. These data were used to estimate the population-level time of onset of spring
115 reproduction (see below). For estimation of population density and population growth rate, we
116 used, in addition, data from September and October. All but six of the datasets originated from
117 monitoring of 0.3 ha trapping grids. The sampling protocol is described in Lambin et al. (2000)
118 and Graham and Lambin (2002). The remaining datasets resulted from monitoring of 1.0 - 1.2
119 ha trapping grids (see methods in Ergon et al. 2001a).

120

121 *Estimation of density and population growth*

122 Most datasets included data from five secondary trapping sessions within each primary session
123 (two to three days of trapping), and abundance estimates were obtained from closed capture-
124 recapture models in program CAPTURE (Rexstad and Burnham 1991). We used a model
125 accounting for temporal variation and individual heterogeneity in capture probability: the M_{th}
126 model of Chao et al. (1992). Abundance estimates from one site in the years 2000 and 2003
127 (site F) and five sites in 2004 (sites F, J, T, U and V) were obtained from robust design models
128 in program MARK (White and Burnham 1999) because these data had been collected with
129 fewer secondary trapping sessions. We here used a model accounting for variation in capture
130 probability depending on time of day (morning/evening) and functional group of the
131 individuals (sex and juvenile/adult). The abundance estimates were converted to density
132 estimates by dividing the estimates by the area covered by the trapping grids including a 5 m
133 boundary strip outside of the outermost traps.

134 As a measure of spring density, we used average density estimates for the months of
135 March and April. For summer densities we used May - June averages, and for autumn densities
136 September - October. Averaging over two consecutive months was done to reduce the variation
137 in the dates (days of the year) for which density estimates were obtained as well as sampling
138 variation in the density estimates (standard deviation of the averaged dates was 10 days for
139 spring, 12 days for summer and 7 days for autumn). We then calculated population growth
140 rates from one season to the next as $\ln(\hat{N}_2 / \hat{N}_1) / \Delta t$, where \hat{N}_2 and \hat{N}_1 are the averaged
141 density estimates for the two seasons, and where Δt is the time between the two averaged
142 dates. We only use population growth rate in a correlation analysis in this paper, but we
143 acknowledge at the outset that our seasonal population growth rates inevitably combine the
144 effects of different processes that may be offset in time. For example, 'population growth' from
145 spring to summer is a variable combination of late winter decline that may sometimes extend

146 into March-April or beyond, and an early-summer increase reflecting the recruitment of the
147 first cohorts of juveniles born in spring. This, though, is true of all such growth rates analyzed
148 in the literature.

149

150 *Estimates of onset of spring reproduction*

151 As a site-level measure of onset of spring reproduction, we used the estimated date when 50 %
152 of the females known to be alive at the site had given birth and were lactating for the first time
153 in the spring. We estimated this with a logistic regression of proportions of postpartum females
154 on sampling date (see methods in Ergon et al. 2001a). Because of the large number of datasets
155 (47) with few trapping occasions per data set (one to six) a model with different slopes would
156 not be supported by the data, hence we used a model with a common slope for all datasets.
157 Confidence intervals around the coefficients of correlation between mean parturition date and
158 estimates of population density and growth rate were obtained by standard non-parametric
159 bootstrapping with 10,000 re-samples.

160 Proportions of animals known to be alive that are postpartum are affected by
161 differences in both capture probability and survival of animals in the two reproductive states.
162 Estimates of capture probability were generally above 80% (Graham and Lambin 2002; Ergon
163 2007; Ergon *et al.* 2009). Although reproducing animals are somewhat more trappable than
164 non-reproducing animals, there is no evidence this difference varies between site and years.
165 Survival differences between pre- and postpartum animals could potentially depend on
166 environmental conditions that vary between sites and years. However, we expect this to have a
167 relatively weak influence on the proportions of postpartum females in the population compared
168 to the extensive variation in this measurement (see below). More sophisticated methods to
169 estimate the latent distribution of individual maturation times from longitudinal capture-
170 recapture data (Ergon *et al.* 2009) were not used because we lacked repeated data on

171 individuals for many of the data sets. For the current analysis, we found it more important to
172 include data from many sites and years.

173

174 *Estimation of density dependence of mean parturition date*

175 We sought to estimate the linear effect of present and previous population densities on onset of
176 spring reproduction. Total Least Squares (TLS) (Van Huffel et al. 2007) is an estimation
177 method well suited for cases with measurement errors in both the predictor (here density) and
178 response variables (here date when 50 % of the females known to be alive at the site had given
179 birth for the first time), particularly as we are interested in the parameters of the model only,
180 not in prediction. In the present case, where the measurement errors differed between data
181 points, we applied the recently developed method Elementwise Weighted Total Least Squares
182 (EW-TLS) (Markovsky *et al.* 2006). This method does not, however, allow for unexplained
183 process variation (i.e., random variation in the expectations between sites and years). We
184 therefore included the EW-TLS fit in a normal likelihood function, with the random process
185 variance being modeled as an exponential of a linear model. The process variance, together
186 with the estimated error variances of the y-values (taken as given), made up the weights used to
187 obtain the EW-TLS fit. This likelihood function was maximized with a simplex method
188 (function ‘fminsearch’) in the Optimization Toolbox of MATLAB (ver. 7.8.0)
189 (<http://www.mathworks.com/>); see Supplementary material Appendix 1 for the Matlab code.
190 Confidence intervals of all parameters were estimated by ordinary non-parametric
191 bootstrapping.

192 It is difficult to implement a model with separate variance components for years and
193 sites in the approach outlined above. To tease these two sources of variation apart, we therefore
194 instead examined the variance components of residuals of the model. Variance components
195 were estimated by the ‘lmer’ function in the ‘lme4’ package (ver. 0.9) of R

196 (<http://cran.r-project.org/web/packages/mcmc>), and HPD confidence intervals were obtained by MCMC-simulations
197 (function 'mcmc' in 'lme4'). Finally, we included the fixed additive effects of year and
198 site in the model to assess potential confounding between these effects and density dependence.

199

200 RESULTS

201

202 Over the 9 years covered by the data (Fig. 1), spring densities at the 22 different sampling sites
203 varied between 27 and 278 voles/ha and autumn densities ranged from 20 to 765 voles/ha
204 (standard error of the density estimates ranged from 2% to 22% of the point estimates).

205 Estimates of the date when 50% of the females known to be alive in a site had given birth for
206 the first time after the winter ranged from March 17 to June 6 (81 days between the extremes).

207 About 15 % of the variance among these estimates was due to measurement error. Within sites
208 in a given year, the estimated time from the date when 5% of the females were postpartum to
209 the date when 95% were postpartum spanned 50 days (95% CI: 46 to 55 days).

210 In Fig. 2, the estimates of mean parturition date are plotted against estimates of past and
211 present population densities, as well as estimates of season specific population growth. Mean
212 parturition date is most strongly correlated with population density in the previous spring
213 (panel A) and population decline during the previous winter season (panel E). Spring
214 reproduction is delayed after high population densities in the previous year and after steep
215 population declines over the previous winter.

216 There is indeed a much larger variation in the population growth rate during the spring
217 than during any other season (note different x-axes in Fig. 2): the standard deviation of
218 population growth rate per time in the spring is 2.8 times higher than in the summer (95%
219 bootstrap CI: 1.8 to 4.2) and 2.9 times higher than in the winter (95% bootstrap CI: 1.8 to 4.4),
220 meaning that relative change in population size over the two spring months varies about as

221 much as the relative change over the four summer months and the six winter months.
222 Furthermore there is a negative correlation between onset of reproduction and population
223 growth during the same spring (March/April to May/June; panel F). There is however no
224 significant correlation between onset of reproduction and population growth during the
225 following summer season (May/June to September/October; panel G).

226 On average, spring reproduction is delayed by 24 days (95 % CI: 13 to 31 days) for
227 every additional 100 voles/ha in the previous spring (Table 1). About 58 % of the variation in
228 mean parturition date (measurement error variance excluded) can be explained by a linear
229 model including past spring densities alone, and the additional effects of past autumn densities
230 and present spring densities do not significantly improve the fit of the regression model (Table
231 1). There is no evidence of delayed reproduction when current spring densities are high. On the
232 contrary, low densities tend to be associated with late reproduction (Table 1) in that steep
233 winter declines (and hence low spring densities) tend to be followed by late onset of
234 reproduction (Fig. 2 panel E).

235 The standard deviation of the unexplained variation among sites and years
236 (measurement error variance excluded) was 11.2 days (95% c.i.: 6.8 to 14.3). Variance
237 component analysis of the residuals of model 1 (Table 1) showed that up to 54 % (point
238 estimate: 25.2 %; 95% c.i.: 0.0 % to 53.3%) of this residual process variance was attributed to
239 between-year variation (e.g. caused by climate effects), whereas less than 10 % of the residual
240 process variance variation (point estimate: 0.0 %; 95% c.i.: 0.0 % to 9.8%) was attributed to
241 between-site variation, possibly reflecting the similar vegetation in each site.

242 Inspection of Fig. 2 shows that a potential confounding between site-differences and
243 delayed density dependent effects is not a concern (note the site labels). On the other hand,
244 year-differences could potentially bias the estimates of density dependence since the
245 populations at the different sites do not fluctuate completely independently (see Fig. 1).
246 However, when ‘year’ was included in the model as a fixed effect, the effect of past spring

247 densities *within* years (parallel slopes model) was still significant and comparable to the overall
248 effect: spring reproduction delayed by 21.5 days (95 % CI: 2.8 to 36.7 days) for every
249 additional 100 voles/ha in the previous spring.

250

251 DISCUSSION

252 Using detailed capture recapture data collected over 9 years in cyclic field vole populations
253 from 22 semi-isolated grassland sites experiencing semi-synchronous dynamics, we detected a
254 very strong effect of previous spring densities (one year lag) on the onset of spring
255 reproduction: the date when 50% of the females had given birth to their first litter of the year
256 varied by more than two months. On average, spring reproduction was delayed by 24 days for
257 every additional 100 voles/ha in the previous spring, where spring densities typically range
258 from about 20 to 300 voles/ha. Considering that female field voles in the spring may give birth
259 repeatedly at about 20 days interval under good conditions (Ergon et al. 2001b), and that
260 offspring born in spring may conceive their first litter immediately after weaning (at 2-3 weeks
261 of age), the potential significance of this variation on population dynamics is substantial.

262 Our analysis also shows that population growth rate is more variable in the spring than
263 in any other season, and that late onset of reproduction is associated with spring declines in
264 population density. This suggests that variation onset of spring reproduction may contribute
265 significantly to the multi-annual density fluctuations in these populations. Although we have
266 not attempted to compare the contributions of the various season-specific demographic
267 processes in this study, we note that other studies in this study system have demonstrated that
268 survival rates vary more between seasons than between years, with lower survival rates in the
269 spring than in other seasons (Graham and Lambin 2002; Burthe *et al.* 2008).

270

271 *Implications for population dynamics*

272 Whereas cyclic phase-specific changes in reproductive traits have long been recognized in
273 cyclic vole populations (Krebs and Myers 1974) as well as in populations of mice with erratic
274 outbreaks (Singelton et al. 2001), the delayed density dependent pattern in the commencement
275 of the breeding season has not previously been quantified. Still, changes in the length and
276 intensity of the summer breeding season have been claimed to be an epiphenomenon of rodent
277 cycles, with little demographic importance (Norrdahl and Korpimaki 2002). In stark contrast,
278 using the same magnitude of delayed density dependence in variation in spring maturation as
279 presented in this paper, Smith *et al.* (2006) formulated analytical models to explore the
280 dynamical implications of delayed density dependent breeding season length and found that
281 these models readily yield 3-4 year cycles similar to those seen in Kielder Forest in terms of
282 periodicity, amplitude and density during the low phase. These models simply assumed that
283 exponential growth takes place over a breeding season of varying length and that populations
284 decay exponentially when no reproduction takes place. The models do not invoke any changes
285 in birth rates or survival. Thus, the combination of empirical and modeling evidence
286 establishes that density dependent feedback acting from spring to spring on a single
287 demographic trait, the relative length of the breeding and non-breeding seasons, may account
288 for the delayed feedback on population growth from one year to the next in multi-annual cycles
289 such as those observed in Kielder Forest (Bierman *et al.* 2006).

290

291 *Potential mechanisms for effects of past densities on onset of spring reproduction*

292 Arvicoline rodents have notoriously flexible life histories, with plastic maturation strategies
293 similar to facultative diapause: individuals may either mature rapidly at a young age (the
294 typical strategy in the spring) or delay maturation for many months until the next breeding
295 season (the typical strategy from mid-summer onward) (Innes and Millar 1995; Ergon et al.
296 2001b). Individuals that delay maturation suspend growth at a sub-adult stage and have a much
297 higher probability of surviving the winter than large voles that have already matured (Hansson

298 1992; Aars and Ims 2002). At the onset of reproduction in the spring, sub-adult voles resume
299 growth and mature rapidly (e.g., Ergon et al. 2001a). In this paper, we have demonstrated a
300 very substantial variation in the time that this onset of spring reproduction takes place.
301 However, we know little about the ecological and physiological mechanisms for this variation,
302 and we only have general ideas about the potential ecological processes that may lead to the
303 delayed density dependent patterns.

304 Mechanisms for delayed density dependence are often separated into intrinsic processes
305 within the population (prolonged changes in the state of the individuals or structure of the
306 population), and extrinsic processes, usually involving trophic interactions. A large scale
307 reciprocal transplant experiment performed in early winter in our study system (Ergon *et al.*
308 2001a) showed that onset of spring reproduction is a function of the immediate environment
309 and not the source population of the individuals. We have thus reasons to believe that intrinsic
310 processes (Chitty 1967) are not important causes of delayed density dependent variation in
311 spring reproduction in our study system. Instead, the memory of past conditions, leading to
312 delayed density dependence in onset of spring reproduction, must reside in the environment
313 experienced by the voles when they initiate reproduction in the spring.

314 It has been suggested that predation may have non-lethal impacts on prey through
315 reduced prey foraging activity when the risk of predation is high, leading to delayed
316 reproduction (Ylönen 1994; Lima 1998). Reduced activity entails lower energy expenditure
317 relative to body mass. However, we have observed the opposite pattern in our study system: in
318 sites where voles commenced spring reproduction late, the voles had substantially elevated
319 field energy expenditure (Ergon *et al.* 2004), despite a smaller body size than in sites where
320 reproduction commenced early. Furthermore, there is no evidence of any time lag between
321 field vole and common weasel dynamics in Kielder Forest (Graham and Lambin 2002). Hence,
322 predation by this specialist vole predator can be dismissed as explanation for the pattern of
323 variation in reproduction reported here.

324 Voles maintain a low body mass through the winter probably due to low energy
325 availability during this time of the year (Hansson 1990; Ergon et al. 2004), and early
326 reproduction is likely to be constrained by limited energy intake during winter/early spring
327 (Bronson and Heideman 1994). Indeed, several food supplement field experiments have
328 succeeded in advancing the onset of the breeding season (reviewed in Boutin 1990), and late
329 onset of reproduction in Kielder field voles appears to be associated with both lower over-
330 winter body mass and slower body growth in the spring (Ergon *et al.* 2001a). Variation in food
331 energy availability during early spring and hence in onset of spring reproduction in voles can
332 be due to variation in the nutritional quality of the early emerging grasses, or it can be due to
333 variation in the phenology of the food plants (i.e., the timing of the emergence of new shoots in
334 the spring). It is well established that reproduction in many species of *Microtus* voles can be
335 triggered by small amounts of the phenolic compound 6-MBOA in their food plants (Berger *et*
336 *al.* 1981; Sanders *et al.* 1981). This compound, which has no nutritional value, is associated
337 with the growth of grasses and thus serves as a cue that enables the voles to initiate
338 reproduction at an early phenological stage of their food plants. Experimental provisioning of
339 6-MBOA to *Microtus townsendii* (Bachman, 1839) populations advanced reproduction by four
340 weeks compared to control (Korn and Taitt 1987). Thus, it is not implausible that some of the
341 substantial between year variation in onset of spring reproduction that we have documented in
342 our study may have been caused by variation in the phenology of the food plants. However, we
343 are not aware of any studies that document any delayed effect of vole grazing on the spring
344 phenology of the food plants, which could potentially cause the delayed density dependence in
345 onset of spring reproduction in the voles. Alternatively, delayed or prolonged reductions in the
346 nutritional quality of the food plants resulting from heavy grazing (Karban and Baldwin 1997),
347 and possibly mediated by induction of silica uptake by grasses may delay the time when voles
348 are able to commence reproduction in early spring (Massey *et al.* 2008).

349 Finally, pathogens such as cowpox and vole tuberculosis are highly prevalent in our
350 study populations (Burthe *et al.* 2008; Telfer *et al.* 2007). Infections by such pathogens are
351 known to delay maturation (Telfer *et al.* 2005) and might thus contribute to variation in the
352 onset of spring reproduction. Since infection state varies among individuals within sites, it is
353 plausible that some of the large variation in onset or reproduction within sites (about 50 days
354 between the 5 % and the 95 % quantiles of the distribution) could be related to pathogenic
355 effects. However, since variation in the mean date for the onset of spring reproduction among
356 sites and years is substantially larger this, pathogens cannot plausibly be responsible alone for
357 the variations at the population level.

358 Hence, while we have identified substantial delayed density dependence in a key
359 demographic trait, the time that spring reproduction commences after the winter, much work
360 remains to be done in identifying the mechanism(s) responsible for this. We stress the potential
361 for synergistic effects between plant responses to grazing and the prevalence and impact of
362 infection by a diverse pathogen community.

363
364 Acknowledgments: This study was funded by NERC grants to XL, a Wellcome Trust
365 grant to MB and XL and the Norwegian Research Council (to TE). We are grateful to the
366 Forestry Commission for providing accommodation and permission to work on their land. We
367 acknowledge the contributions of Sarah Burthe, James L MacKinnon, Isla M. Graham and
368 David Tidhar to vole trapping, and we thank Ivan Markovsky for advising us on the use of the
369 EW-TLS procedure.

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Table 1. Parameter estimates [95% confidence intervals] for different models of mean parturition date. Confidence intervals that do not include zero are in bold.

Model	Intercept (SE in days)	Past spring density (days per 100 voles/ha)	Past autumn density (days per 100 voles/ha)	Present density (days per 100 voles/ha)	Random variation* (SD in days)	Proportion of variance explained†
1. Past spring density (PSD)	20. Mar (6.4)	23.9 [12.7, 30.7]			11.2 [6.8, 14.3]	0.58
2. Past autumn density (PAD)	06. Apr (5.5)		4.8 [0.0, 8.2]		13.6 [9.1, 16.2]	0.25
3. Present density (PrD)	26. Apr (5.7)			-7.8 [-17.4, 0.9]	15.5 [11.5, 18.9]	0.07
4. PSD + PAD	21. Mar (7.0)	25.6 [9.2, 42.2]	-0.9 [-6.6, 4.9]		11.3 [5.9, 14.2]	0.57
5. PSD + PrD	01. Apr (9.0)	24.1 [16.0, 31.1]		-8.8 [-17.0, 2.0]	10.6 [5.9, 13.5]	0.63
6. PAD + PrD	18. Apr (6.8)		6.4 [2.2, 9.5]	-13.5 [-24.7, 0.2]	12.1 [7.9, 14.3]	0.42
7. PSD + PAD + PrD	04. Apr (13.1)	20.3 [1.1, 41.1]	1.5 [-6.8, 8.9]	-10.1 [-26.9, 5.4]	10.7 [5.2, 13.2]	0.65

* Estimated unexplained random variation (measurement error excluded) among site×years expressed as standard deviation (unit of days).

† Proportion of total process variance (estimated measurement error variance subtracted) explained by the model. Values are not directly comparable across models because slightly different subset of the data are used due to missing values in the predictor variables.

Figure 1. Population density estimates at the 22 sampling sites (labels A to V) during spring (S) and autumn (A) plotted on a linear scale (panel a) and on a log-scale (panel b). Top left inset shows estimates of spring (open symbols) and autumn (filled symbols) densities averaged over minimum 18 sites in the Kielder forest region per year (methods in Lambin et al 2000).

Figure 2. Estimated dates when 50% of the females in a site were post-partum in year t plotted against estimates of A) density in the previous spring (March/April of year $t-1$), B) density in the previous autumn (September/October of year $t-1$), C) density in the present spring (March/April of year t), D) population growth from May/June to September/October in year $t-1$, E) population growth from September/October in year $t-1$ to March/April in year t , F) population growth from March/April to May/June in year t , and G) population growth from May/June to September/October in year t . Population growth rates are on a monthly time-scale. Error bars show \pm SE (when missing, SE is smaller than the symbol). Plotted labels represent site (letters corresponding to the labels in Fig. 1) and year (numbers; 1 = 1996, ..., 9 = 2004). 95% bootstrap confidence intervals of correlation coefficients are given at the top of each panel.

Figure 1.

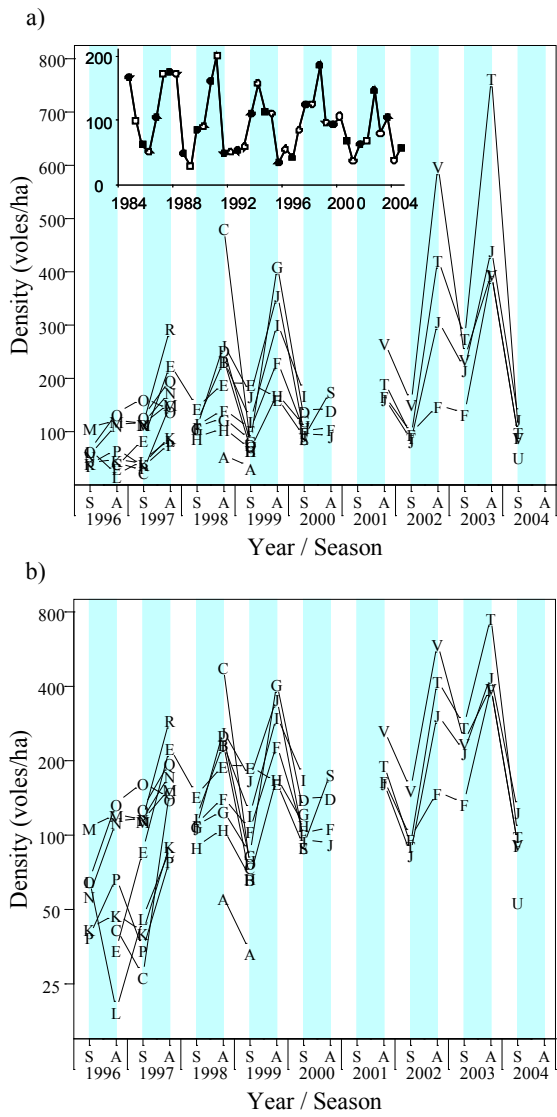
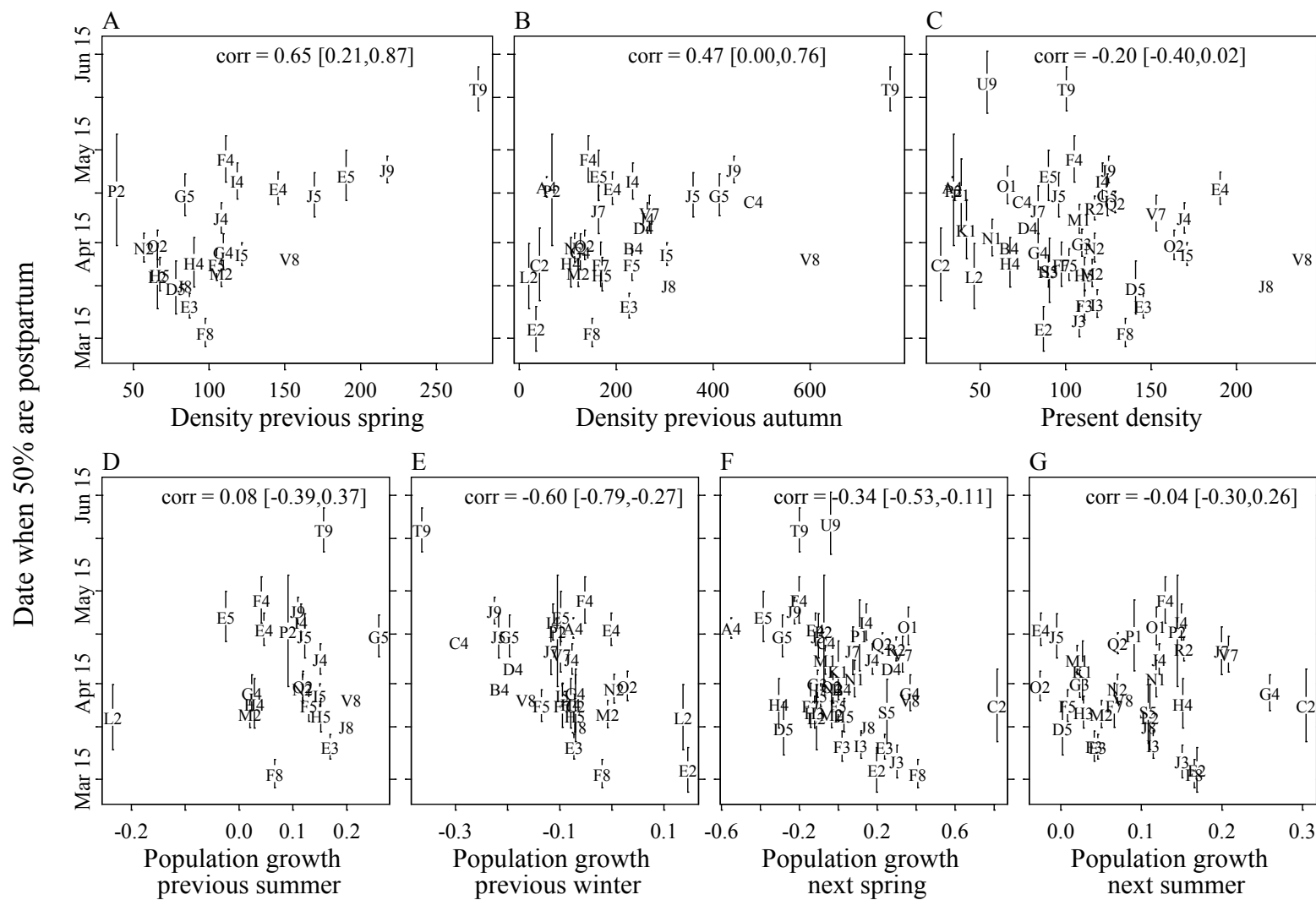


Figure 2



APPENDIX 1 (for Supplementary material on Oikos' homepage)

MATLAB code used to estimate density dependence in the paper. The code makes use of the 'ewtls' function by Markovsky et al. (2005) at

<ftp://ftp.esat.kuleuven.ac.be/pub/SISTA/markovsky/reports/02-48c.m>

```
function [a,b,nll,ex,out] = EWTLSrandom(Xvar,Xfix,seX,seY,Y,b0)
% Fits a linear regression model by EWTLS (fixed effects) and maximum
% likelihood (random component). Elementwise (observationwise)
% variation in the precision in both x and y values are allowed
% (assumed given and must be supplied). The random residual component
% is fitted as an exponential of a linear model.
% Note that the random residual component is part of the weights in
% the EWTLS.
%
% Input:
% Xvar = model matrix for v0 (= between site variance).
% Xfix = model matrix for E[Y] at a mean site.
% seX = standard errors of the X-values (same dimensions as Xfix - typically
% zero for intercept).
% seY = standard error of the Y-values.
% Y = response variable (dependent variable).
% b0 = starting values of the random effects parameters.
%
% Output:
% a = fixed effects parameters (from final EWTLS fit).
% b = log-link parameters for the model of v0.
% [nll,ex,out] = negative log-likelihood, exit flag and output from
% 'fminsearch'.

[b,nll,ex,out] = fminsearch(@nllEWTLSrandom, b0, [], Xvar, Xfix, seX, seY,
Y);

% Retrieving the fixed parameters from the final fit:
v0 = exp(Xvar*b);
vtot = seY.^2+v0;
s = [seX, sqrt(vtot)];
a = ewtls(Xfix, Y, s);

function f = nllEWTLSrandom(b,Xvar,Xfix,seX,seY,Y)
% Negative log-likelihood of EWTLS fit with an exponential random
% residual component

% Fitting EWTLS
v0 = exp(Xvar*b); % Between site variance
vtot = seY.^2+v0; % Total residual variance
s = [seX, sqrt(vtot)];
a = ewtls(Xfix, Y, s); % from
%ftp://ftp.esat.kuleuven.ac.be/pub/SISTA/markovsky/reports/02-48c.m

% Computing the negative log-likelihood
dy = Y - Xfix*a;
f = -sum(-log(sqrt(vtot)) - dy.^2./(2.*vtot));
```