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Age structure and movement of Capercaillie (*Tetrao urogallus*) males in NW Russia – a two-compartment model

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Capercaillie (*Tetrao urogallus*) males in the remnant unlogged forest of NW Russia have an unusual age structure, with more older than younger birds. In logged forest, the more normal opposite occurs. A possible explanation involves two-way movement in which youngsters disperse from unlogged to logged forest and older birds, up to their third spring, do the reverse. As Capercaillie cocks do not generally attain mating status until their third spring or later, both movements could be classed as natal dispersal. We develop a two-compartment population model that shows how this could happen and make a first approximation of the numbers and distances that would be involved. The model highlights gaps in knowledge that should be addressed by further fieldwork.

1. Introduction

Capercaillie, the biggest of grouse, mostly live in old coniferous forest, where they display together in spring at traditional mating arenas called leks (Wegge & Larsen 1987). Some authors consider these polygamous birds to be mainly sedentary (Semenov-Tian-Shansky 1960, Romanov 1979, Potapov 1985). Nonetheless, many Capercaillie shift between summer and winter ranges, seasonal movements of adult radio-tagged birds in western and central Europe averaging 1–2 km with maximum distances of 10 km or more (Storch 2001). Elsewhere, in parts of the Urals, Kazakhstan and Siberia, seasonal migrations of tens of km occur between winter and summer habitats (Kirikov 1952, Kuzmina 1968, Potapov & Sale 2013). Such variations are broadly consistent with the "landscape mosaic" hypothesis (Rolstad & Wegge 1989), in which longer seasonal movements occur in coarser-grained landscapes with less habitat interspersion (Hjeljord *et al.* 2000). Also, there are suggestions of long-distance irruptive movements, some over 1,000 km (Couturier & Couturier 1980, Cramp & Simmons 1980, Potapov 1985, Liukkonen-Anttila *et al.* 2004). In Finland, Siivonen (1952) considered periodic "migrations ... of a mass character" to be characteristic of Capercaillie and other tetraonid population fluctuations, although the birds were then more numerous than now.

Borchtchevski & Moss (2014), after Borchtchevski (1993), proposed a novel pattern of age-related movement in a forest landscape much modified by intensive clear-cutting (Aksenov *et al.* 2002). Their hypothesis came from the obser-

Table 1. Age distribution of cock Capercaillie (percent of total cocks > 11 months old) from logged and native forest in NW Russia, sampled in 1980–2008. *CI* = 95% confidence interval. Based on data for late summer, winter and spring from Fig. 3 of Borchtchevski & Moss (2014). Age class 0 is excluded (see section 2).

Age class	Age in months	Logged habitat		Native habitat	
		Percent	*CI*	Percent	*CI*
1	12–23	49	40–59	11	7–16
2	24–35	28	22–36	21	16–28
3	36–47	15	11–22	44	36–54
4	> 48	10	6–16	25	19–33

vation that the age distribution of males in remnant unlogged native forest in NW Russia was unbalanced, with more 2- and 3-year-old males than yearlings in late summer, winter and spring (Table 1). In logged forest, by contrast, they found fewer old males than yearlings – as expected when some birds of each age die every year. In explanation, they proposed a “two-compartment” or “two-way” model with two streams of movement: 1) recently-reared youngsters emigrating from native to logged areas in late summer and 2) a reverse movement of maturing cocks attempting to join the bigger leks on native areas, most probably in early spring.

This raises questions about the numbers of birds expected in each stream and compartment, and the areas of the latter. We explore these issues via a mechanistic model, check whether it is consistent with known facts, and use it to provide conditional estimates of bird numbers in each stream and compartment.

1.2. Population model

1.2.1. Outline

The coarse-grained landscape comprises discrete tracts of native forest within vast logged areas. The former supports higher densities of Capercaillie, sparser and older trees, plus a field layer with much blueberry (*Vaccinium* spp.). In logged forest, trees regrow more densely after clear-cutting while the field layer is dominated by forbs and grasses. Also, people – including hunters – occur much more frequently (Borchtchevski & Moss 2014).

We represent these habitat types as two compartments in a population model based on age-specific population growth rates, with a time step of one year. It shows how recruitment, movement and death together result in specific age structures. Output includes relative numbers of each age class living in and moving between the two compartments, plus the relative areas of the latter. The model describes an average situation based on the age distributions of birds collected in 1980–2008; it has no annual variation and no explicit representation of distance, which is considered separately. We assume for parsimony that population parameters have the same values in both compartments unless there is contrary evidence.

1.2.2. Definitions

Spring numbers (P) of cocks in native (N) and logged (L) compartments comprise five age classes (i, 0–4, the latter including all ages ≥ 4 years). Their numbers (P_{Ni} and P_{Li}) embrace both cohort-specific (horizontal) and time-specific (vertical) age structures (Table 2). Total spring populations in N and L are $P_{N0\rightarrow4}$ and $P_{L0\rightarrow4}$.

Age-specific annual population growth rate G is prospective, for example $G_{N1} = P_{N2} / P_{N1}$ and $G_{L1} = P_{L2} / P_{L1}$. Age-specific annual survival rate S, also prospective, is the proportion of a given set of birds that survives from one spring to the next. For age classes (0, 3 and 4) showing no net movement between compartments, $S = G$. For other age classes (1 and 2), S and G differ due to movement. We parsimoniously assume that $S_{N0} = S_{L0} = S_0 = G_0$, $S_{N1} = S_{L1} = S_1$ and $S_{N2} = S_{L2} = S_2$.

Movement stream 1 (M_1) involves movement

Table 2. Two-compartment population model – definitions. Input parameters needed to run the model are marked with an asterisk (*).

Basic model		
N		Native forest compartment
L		Logged forest compartment
P		Population number
i		Age class, from 0 (cocks in their first spring) to 4 (cocks in their fifth spring and older)
P_{Ni}		Number of cocks in N of age class i. Similarly P_{Li} for L
P_{NB}		Total number of hens in N. Similarly, P_{LB} for L
G_{Ni}	*	Age-specific population growth rate P_{Ni+1} / P_{Ni} in N, similarly $G_{Li} = P_{Li+1} / P_{Li}$
S_{Ni}	*	Age-specific survival – the proportion of spring cocks in N of age i that survive until spring $i + 1$, whether in N or L. Similarly for age i cocks in L. S_i – joint value for N and L
k_S	*	S_0 / S_1
y	*	Average number of young cocks per hen in late summer, the same in N and L
S_y		Proportion of y that survives until spring, the same in N and L
e		Proportion of young cocks, in N in late summer, destined for emigration to L
M_{1em}		Number of young cocks set to leave N in movement stream 1
M_{1im}		Number of M_{1em} that survive until spring
M_{2em}		Number of cocks set to leave L in movement stream 2
M_{2im}		Number of M_{2em} that survive until spring
Incorporate area		
k_d	*	Spring density of cocks N / L, based on field observations
k_N	*	The areal percentage of N used by Capercaillie
A_N		The area of N as a percentage of $N + L$, with $k_N = 1$
A_{N1}		As A_N but $k_N < 1$. Numbers in N and L remain the same, but the area of N is increased by $1 / k_N$
A_{N2}		As $A_{N1,}$ but the area of native forest not used by caper is classed as part of L

of newly-reared youngsters from N to L during or after their first summer. Their survival between late summer and spring, when P_{N0} and P_{L0} are defined, is S_y. Stream 2 (M_2) involves a reverse movement, from L to N, of age classes 1 and 2 between springs 1–2 and 2–3 respectively, their corresponding survival rates being S_1 and S_2.

1.2.3. Stream 1

Cocks play no part in rearing young. The number of hens (P_{NB} and P_{LB}) and the average number of young cocks each rears (y) determine the number reared in N and L respectively. Hens rearing chicks may be distributed differently from full-grown cocks but, absent better data, we estimate P_{NB} and P_{LB} from $P_{N0\to4}$ and $P_{L0\to4}$. Stream 1 shrinks from $P_{NB} \times y \times e$ (newly-reared young in N in late summer and set to emigrate, M_{1em}) to $P_{NB} \times y \times e \times S_y$ (the same young after they have emigrated to L and suffered autumn and winter mortality, M_{1im}) where $S_y = (P_{N0} + P_{L0}) / (y \times (P_{N0\to4} + P_{L0\to4}))$.

The proportion of young that emigrates from N to L (e) is found as follows:

(spring young in N after emigrants leave) / (spring young in L after immigrants arrive) $= (P_{NB} \times y \times S_y \times (1 - e)) / ((P_{LB} \times y \times S_y) + (P_{NB} \times y \times S_y \times e)) = P_{N0} / P_{L0}$

so that

$$(P_{NB} \times (1 - e)) / (P_{LB} + P_{NB} \times e) = P_{N0} / P_{L0}. \tag{1}$$

For convenience, we set $P_{N1} = 1$ such that the working unit is P_{N1}. As $P_{N0} / P_{L0} = P_{N1} / P_{L1}$,

$$e = (P_{L1} \times P_{NB} - P_{LB}) / (P_{NB} \times (1 + P_{L1})). \tag{2}$$

1.2.4. Stream 2

Some birds from age classes 1 and 2 move from L to N. Hence

$$P_{L1} \times (S_1 - G_{L1}) = P_{N1} \times (G_{N1} - S_1), \tag{3}$$

where $G_{N1} > S_1 > G_{L1}$ and $S_1 < 1$. So

$$P_{L1} / P_{N1} = (G_{N1} - S_1) / (S_1 - G_{L1}). \tag{4}$$

Similarly

$$P_{L2} / P_{N2} = (G_{N2} - S_2) / (S_2 - G_{L2}). \tag{5}$$

By definition, $P_{L1} \times G_{L1} = P_{L2}$ and $P_{N1} \times G_{N1} = P_{N2}$. From Eqs 4 and 5

$$S_2 = S_1 \times (G_{L1} \times G_{L2} - G_{N1} \times G_{N2})\,(G_{L1} \times G_{N1}) \times (G_{N2} - G_{L2}) / (S_1 \times (G_{L1} - G_{N1})). \tag{6}$$

Hence, knowing G_{L1} and G_{L2} and specifying S_1, we can estimate the numbers from age classes 1 and 2 that immigrate into *N* and survive until the following spring as

$$M_{2im} = P_{L1} \times (S_1 - G_{L1}) + P_{L1} \times G_{L1} \times (S_2 - G_{L2}). \tag{7}$$

Numbers in spring and set to emigrate from *L* (M_{2em}) are M_{2im} / S_2

1.2.5. Compartment areas

In the two-compartment model, the areal proportion of good Capercaillie habitat $N / (N + L)$ is

$$A_N = P_{N0\to4} / (P_{N0\to4} + k_d \times P_{L0\to4}), \tag{8}$$

where k_d is the spring density of cocks in N / L.

In reality, however, there is a third habitat type. Unlogged ground with few Capercaillie includes the centres of open bogs and tundra, while closed canopy spruce (*Picea* spp.) with mossy ground cover (Borchtchevski 1989, 2003; Borchtchevski & Moss 2008) occupies much of the riverine watershed. Some native tracts (e.g., the one northeast of Plesetsk in Fig. 1 of Borchtchevski & Moss 2014) consist largely of monotonous, uniform and relatively dense spruce forests likely to support low densities of Capercaillie. Also, snow melt is late in spruce forests, especially in the extreme north east of NW Russia (Mil'kov & Gvozdetskiy 1976), so making the snow-free season too short for nesting and chick rearing. We therefore assume that a proportion k_N of real unlogged forest is used by Capercaillie and equivalent to compartment *N*, while other unlogged ground is unused. Thus, the observed (Aksenov *et al.* 2002) areal proportion of all unlogged forest including *N* and "other unlogged ground" becomes

$$A_{N1} = (P_{N0\to4} / k_N) / (P_{N0\to4} + k_d \times P_{L0\to4}). \tag{9}$$

Alternatively, if Capercaillie use "other unlogged ground" as if it were *L*,

$$A_{N2} = (P_{N0\to4} / k_N) / (P_{N0\to4} + k_d \times P_{L0\to4} - P_{N0\to4} \times (1 - 1 / k_N)). \tag{10}$$

1.2.6. Input parameter values

To get numerical output from the model we input age-specific values for *G* and *S* plus a value for *y*. Then, to estimate the relative areas of the two compartments, we input values for k_d and k_N. Up to this point, output is measured relative to P_{N1}. To get output in whole numbers we note that P_{N1} is a defined proportion of $P_{N0\to4}$ and assign a numerical value to $P_{N0\to4}$.

Borchtchevski & Moss (2014) provided three season-based (summer–summer, winter–winter and spring–spring) estimates for each of the age-specific population growth rates G_{N1}, G_{N2}, G_{L1} and G_{L2} (their Table 3) plus (their Table 4) G_{N3} and G_{L3}, which applied to all ages ≥ 3. They cautioned, however, that their estimates of G_{N0} and G_{L0} (and hence our G_0) were flawed by sampling biases in age class 0. Other than G_0, each of our "original" *G* values is a mean of their three season-based estimates.

Age-specific annual survival rates *S* are the same as *G* for some age classes. Model age classes 4, 3 and 0 show no net movement between compartments such that $S_{N3} = G_{N3}$ and $S_{L3} = G_{L3}$. Similarly, $S_0 = G_0$ but, having no direct measurement of either, we put $S_0 = k_S \times S_1$ where k_S is a constant initially set equal to 1. Age classes 1 and 2 take part in stream 2 so $S_1 \neq G_1$ and $S_2 \neq G_2$, which means that we have no direct measurements of S_1 and S_2. Eq. 6, however, defines S_2 as a function of S_1, G_{L1}, G_{L2}, G_{N1} and G_{N2}. Therefore, knowing G_{L1}, G_{L2}, G_{N1} and G_{N2} (previous paragraph), we ran the model with a range of values for S_1 – as detailed at the end of this section.

The median number of chicks reared per hen in 17 studies through much of the birds' range was 1.6 (Moss *et al.* 2000). Studies in NW Russia indicate an average of just over two (Desbrosses *et al.* 1992, Borchtchevski 1993 & unpubl., Borchtchevski *et al.* 2003) while their sex ratio tends to favour females, in NW Russia (Borchtchevski unpubl.) as elsewhere (Hörnfeldt *et al.* 2001). Our initial value for y is therefore 1. The density of both sexes combined in N has been estimated as ~ 2 / km^2 and in L ~ 0.6 / km^2 (Borchtchevski & Moss 2014) so that, assuming a 50:50 sex ratio, $k_d \sim 3.33$. We discuss densities (section 4.1).

About 25% of remnant intact native forest landscapes in Russia comprise open ground (Aksenov *et al.* 2002), and dense native spruce tracts (section 1.2.5) are likely to support low densities of Capercaillie. We therefore estimate k_N as 0.5, bearing in mind that this is likely to change with better information. Next, the proportion of remnant native forest (Aksenov *et al.* 2002) in the studied part of NW Russia includes that in the Archangelsk Region, the Nenets Autonomous District, and the Republics of Komi and Karelia. This amounts to ~ 200,000–250,000 km^2 of a total forest area of ~ 810,000–860,000 km^2 (25–29%). With $k_N = 0.5$, the equivalent of model compartment N is ~ 112,500 km^2. For simplicity, when illustrating model output in concrete bird numbers we round this to 100,000 km^2. As spring cock density in N is ~ 1 / km^2 (previous paragraph), such output is based on 100,000 spring cocks in N and $100{,}000 \times P_{L0\to4} / P_{N0\to4}$ in L.

Eq. 6 defines S_2 as a function of S_1, G_{L1}, G_{L2}, G_{N1} and G_{N2}. For each realistic value of S_1 we used three criteria to exclude unrealistic values of S_2 and to investigate whether it was necessary to vary the original estimates for G_{N1}, G_{N2}, G_{L1} or G_{L2}. We kept G_{N3}, G_{L3}, y, k_S, k_d and k_N as above.

- First, four telemetry studies in western and central Europe (Storch 2001) showed average survival rates of cocks > 12 months old to be 0.70–0.84. Hence we aimed for values of S_1 and S_2 within a biologically plausible range of 0.65–0.90.
- Second, we know of no evidence that S_1 differs materially from S_2 and so a model with $S_1 \approx S_2$ over the range 0.65–0.90 was preferred.
- Third, the areal proportion of unlogged forest (A_{N1} or A_{N2}) should be ~ 25–29% (Aksenov *et al.* 2002).

Sensitivity analyses then varied the four G estimates by ± 20%, one at a time, for each value of S_1 in the range 0.65–0.90. Outputs for S_2, A_{N1} and A_{N2} were checked against the criteria, so pointing to parameter sets with realistic output. Below, we give illustrative output using one such parameter set. For simplicity, we preferred a set with not more than one G value altered from the original.

1.3. Distance model

We consider movement distances via a distinct, spatially explicit two-compartment model comprising four concentric circles with radii $n < 1 < g < f$. Compartment N includes the inner disc and adjacent annulus, compartment L the outer two annuli. Within N and L respectively, the two sub-compartments are equal in area and birds are positioned randomly. On average, a random selection of bird positions within a compartment has its median on the circle separating sub-compartments. The median migrant moves between random positions on the two separators, a straight-line distance between $g - n$ and $g + n$, average g. Hence $n = \sqrt{0.5}$, $g = \sqrt{[(1 / 2A_N) + 0.5]}$ and $f = \sqrt{(1 / A_N)}$. The average distance moved is $\sqrt{[(1 / 2A_N) + 0.5]} \times$ (radius of native forest compartment if ≠ 1). For realistic estimates, substitute A_{N1} or A_{N2} for A_N.

2. Statistical methods

Table 1 shows output from a simplified analysis of the data in Fig. 3 of Borchtchevski & Moss (2014). We followed their modelling approach but dropped age class 0 (< 12 months), which suffered from season-related sampling biases. Also, we combined results for their three seasons (summer, winter, spring) as follows. The unit of analysis (individual bars in their Fig. 3) in a generalised linear mixed model (GLMM) was the number of cocks categorised by age class (1–4), study area (two in logged, two in native habitat) and season. The

Table 3. Sensitivity analysis: how variations in G (central value ± 20%) influence the relationship between S_1 (survival of age class 1) and S_2 (Eq. 6).

Input	Output S_2					
S_1	Central G values		G_{N1}	G_{N2}	G_{L1}	G_{L2}
0.65	0.68*	0.63	0.64–0.63	0.61–0.66	0.81–0.43	0.53–0.74
0.70	0.79*	0.70	0.72–0.69	0.66–0.75	0.86–0.52	0.61–0.80
0.75	0.89*	0.76	0.78–0.75	0.69–0.83	0.90–0.60	0.68–0.85
0.80	0.98*	0.81	0.84–0.80	0.73–0.90	0.94–0.67	0.74–0.89
0.85	1.06*	0.86	0.89–0.84	0.76–0.96	0.98–0.73	0.79–0.93
0.90	1.13*	0.90	0.94–0.88	0.78–1.02	1.01–0.78	0.84–0.96

* With $G_{N1} = 2.1$, $G_{N2} = 1.8$ (original value), $G_{L1} = 0.61$, $G_{L2} = 0.57$. In the next column, central G values were the same except that $G_{N2} = 1.3$ (illustrative model). There was no effect of G_{N3} (0.42) and G_{L3} (0.37) on S_2.

GLMM, with Poisson distribution and log link, was corrected for any extra-dispersion. The response variable was the number of cocks in each unit of analysis offset by the natural logarithm of the total number of cocks in all four age classes, categorised by study area and season. Fixed effects were age class, habitat and season. Random effects included main year and main method of sampling (Borchtchevski & Moss 2014) but, as each covariance parameter estimate was < 0, the GLMM reverted to a generalised linear model (GLM). Also, season ($F_{2,25} = 0.29$, $P = 0.75$) and its interactions with habitat ($F_{2,25} = 0.14$, $P = 0.87$) and age class ($F_{6,25} = 1.09$, $P = 0.40$) were insignificant (SAS [ver. 9.1] type 3 [partial] F-test). Hence we dropped season and used a GLM with fixed effects habitat ($F_{1,36} = 0.20$, $P = 0.65$) and age class ($F_{3,36} = 3.2$, $P = 0.034$), plus their interaction ($F_{1,36} = 29.5$, $P < 0.0001$), to estimate the percentages shown in Table 1.

We used output from the same GLM when simulating approximate 95% confidence intervals (*CI*) for modelled population and stream sizes. GLM output included the mean and standard error (*SE*) of the proportion of age class i (where $i = 1$–4) in each habitat (A_{Ni} or A_{Li}). We used these, in effect, to reconstitute a normal distribution for each age class, from which we selected and ranked 10,000 random samples (rsA_{Ni} or rsA_{Li}). Simulated *CI* were given by ranks 250 and 9,750. For a more complex parameter such as $G_{N1} = P_{N2}/P_{N1} = A_{N2}/A_{N1}$ we simulated rsA_{N2}/rsA_{N1} 10,000 times and thence calculated its simulated *SE*. Simulated means typically differed slightly from the equivalent value in the illustrative model and so, for calculations based on this model (for example, $rsG_{N1} - rsS_1$), we used the illustrative central values together with the simulated *SE*s. Variations in survival S_1 were simulated via logit $rsS_1 = \log_e(S_1 / (1 - 0.80) + rs(0.9))$, which avoided $rsS_1 > 1.0$ and gave $S_1 = 0.80$ (*CI* 0.69–0.85, which embraced the observed range of 0.70–0.84 (Storch 2001)). We were as uncertain about the mean value of y as about its variance and so used a uniform distribution in the range 0.6–1.4 to generate $rs(y)$. Output was for numbers of birds in P_{N1} units, which we converted to birds per 100,000 spring cocks in N (section 1.2.6). As these results involve numbers of birds but not compartment areas, they are unaffected by k_d and k_N. Fuller details of *CI* simulations are in the Appendix.

3. Results

Age structures generated by the model depend on age-specific population growth rates G, themselves based on those previously estimated (Borchtchevski & Moss 2014) from observed age distributions (Table 1). It is therefore inevitable that modelled age structures (Table 5) resemble observed ones. Our primary aim is to explore how big relative population sizes ($P_{N0\rightarrow4}$ and $P_{L0\rightarrow4}$) and movement streams (M_1 and M_2) must be to generate the salient age structure in N. We start by checking which values of G and S conform with the three reality criteria (section 1.2.6) and the constraints imposed by the model.

Table 4. Sensitivity analysis for illustrative model: effect of varying S_1 (survival of age class 1) on S_2, population size, relative compartment size, first-winter survival and movement streams.

Input	Output									
S_1	S_2	$P_{N0\to4}$	$P_{L0\to4}$	A_N	A_{N1}	A_{N2}	S_y	e	M_{1em}	M_{2em}
0.65	0.63	9.32	105.9	2.0	4.1	4.2	0.39	0.59	5.49	4.44
0.70	0.70	9.24	55.9	4.7	9.5	9.9	0.36	0.57	5.30	3.79
0.75	0.76	9.16	36.8	7.5	15.0	16.3	0.34	0.56	5.11	3.28
0.80	0.81	9.07	25.0	10.4	20.9	23.3	0.31	0.54	4.92	2.88
0.85	0.86	9.00	18.4	13.4	26.9	31.0	0.28	0.53	4.74	2.54
0.90	0.90	8.92	13.5	16.5	33.0	39.5	0.25	0.51	4.55	2.26

Population size and movement streams in P_{N1} units.

3.1. Realistic parameter values

Equation 6 defines S_2 as a function of S_1, G_{N1}, G_{N2}, G_{L1} and G_{L2}. Thus, for a given set of G values, solutions to Eq. 6 comprise paired values of S_1 and S_2. Unconstrained, this allows S_2 to differ widely from S_1, which is unrealistic (section 1.2.6). For example, given the original G values (Table 3), the solution when $S_1 = S_2$ is 0.63, such that $A_{N1} \approx A_{N2} = 0.02$ or 2%. Above 0.63, S_2 increases twice as fast as S_1 (Table 3), such that when $S_1 > 0.81$, $S_2 > 1.00$, which is impossible. The original G set therefore fails all three reality criteria, the second two badly, and so we alter it minimally. The sole single adjustment that fulfils the three criteria is to decrease G_{N2}. Reducing it from the original 1.8 to 1.3 gives values of S_1 and S_2 agreeing within 0.02 over the range 0.65–0.90 (Table 3). Versions of the model with $G_{N2} = 1.3$ and S_1 varying from 0.80 to 0.85 each give similarly realistic output for A_{N1} or A_{N2}

Table 5. Sensitivity analysis for illustrative model: how variations in G (central value ± 20%) influence age structures in N and L, movement streams M_1 and M_2 and the proportion of native forest A_N.

Parameter	Central	G_{N1}	G_{N2}	G_{L1}	G_{L2}
P_{N0}	1.25	–	–	–	–
P_{N1}	1.00	–	–	–	–
P_{N2}	2.10	1.68–2.52	–	–	–
P_{N3}	2.73	2.18–3.28	2.18–3.28	–	–
P_{N4}	1.98	1.58–2.37	1.58–2.37	–	–
$P_{N0\to4}$	9.06	7.70–10.4	8.12–10.0	–	–
P_{L0}	8.55	5.79–11.3	–	5.21–23.9	–
P_{L1}	6.84	4.63–9.05	–	4.17–19.1	–
P_{L2}	4.17	2.83–5.52	–	2.03–14.0	–
P_{L3}	2.38	1.61–3.15	–	1.16–7.98	1.90–2.85
P_{L4}	1.40	0.95–1.85	–	0.68–4.68	1.12–1.68
$P_{L0\to4}$	23.3	15.8–30.9	–	13.3–69.7	22.6–24.1
e	0.54	0.46–0.61	0.51–0.57	0.52–0.57	0.55–0.53
S_y	0.30	0.30–0.30	0.31–0.29	0.29–0.32	0.31–0.30
M_{1em}	4.92	3.52–6.31	4.10–5.75	4.74–5.14	5.02–4.83
M_{2em}	2.88	1.95–3.81	–	2.24–5.82	3.46–2.29
A_N	10.4	12.8–9.2	9.5–11.4	17.0–3.76	10.8–10.1
A_{N1}	20.9	25.5–18.4	18.9–22.8	34.1–7.51	21.5–20.3
A_{N2}	23.3	29.3–20.3	20.9–25.7	41.1–7.81	24.1–22.6

– = No change from central value as heading G not used in calculating this output.
Central values $G_{N1} = 2.1$, $G_{N2} = 1.3$, $G_{L1} = 0.61$, $G_{L2} = 0.57$, $G_{L3} = 0.37$ with $S_1 = 0.80$. S_2 was held constant at the value found using these central values. All results relative to $P_{N1} = 1$. Effects of variations in G_{N3} and G_{L3}, which were less germane, can be seen in Table 7 plus the Excel spreadsheet provided as online supplementary material.
M_{1em} stream 1 emigrants from N, M_{2em} stream 2 emigrants from L.

Table 6. Sensitivity analyses for illustrative model: impacts of variations in k_S, y, k_d and k_N (central value ± 20%).

Output	Input				
	Central	k_S	y	k_d	k_N
$P_{N0\to4}$	9.06	9.37–8.85	–	–	–
$P_{L0\to4}$	23.3	25.5–21.9	–	–	–
S_y	0.30	0.35–0.27	0.38–0.25	–	–
M_{1em}	4.92	–	3.94–5.91	–	–
M_{1im}	1.49	1.73–1.31	–	–	–
A_N	10.4	9.9–10.8	–	12.7–8.8	–
A_{N1}	20.9	19.9–21.6	–	25.4–17.7	26.1–17.4
A_{N2}	23.3	22.1–24.2	–	29.1–19.4	30.9–18.7

– = No effect as heading not used in calculating this output.

(Table 4). We therefore adopt an illustrative version of the model with G_{N1}, G_{L1} and G_{L2} as in the original G set, $G_{N2} = 1.3$ and $S_1 = 0.80$. Readers may investigate other parameter values via the Excel spreadsheet provided as online supplementary material.

3.2. Population dynamics in *N* and *L*

The unbalanced age structure in *N* is maintained largely by stream 2 (M_2). A notable feature of model output is that population size $P_{L0\to4}$ varies much more than $P_{N0\to4}$, especially with S_1 (Table 4) and G_{L1} (Table 5). Broadly, a fairly constant $P_{N0\to4}$ requires a fairly constant M_2 to maintain its age structure: hence if M_2 as a proportion of $P_{L0\to4}$ declines then $P_{L0\to4}$ itself must increase. More specifically, M_2 depends (Eq. 7) partly on differences between S and G in age classes 1 ($S_1 - G_{L1}$) and 2 ($S_2 - G_{L2}$) and partly on the numbers of birds in these classes (P_{L1} and $P_{L2} = G_{L1} \times P_{L1}$). Hence decreases in S_1 and S_2 tend to depress M_2 but this is counteracted by increases in P_{L1} (Eq. 4) and P_{L2} (Eq. 5) and consequently $P_{L0\to4}$. Again, decreases in G_{L1} tend to depress M_2 (via its effect on age class 2, Eq. 7) but this is offset by increases in P_{L1} (Eq. 4) and so $P_{L0\to4}$.

The area of forest needed to support $P_{L0\to4}$ depends not only upon bird numbers but also upon their density. Thus A_N falls as $P_{L0\to4} / P_{N0\to4}$ rises (Eq. 8) and falls further as k_d increases (Table 6). The fact that native forest includes some ground with low densities of Capercaillie is modelled by A_{N1} or A_{N2} increasing as k_N falls.

The unbalanced age structure in *N* involves relatively low P_{N0} and P_{N1}, which occur partly because M_2 enhances P_{N2} and P_{N3}. The hypothesis (Borchtchevski & Moss 2014) also suggests that P_{N0} and hence P_{N1} are further depressed by M_1, emigration of newly-reared young. In the model, M_1 and M_2 are calculated independently of each other. Thus, the number of youngsters reared in *N* is $P_{N0\to4} \times y$ and the number emigrating in stream 1 is $M_{1em} = P_{N0\to4} \times y \times e$. Overwinter mortality S_y is determined by the number of surviving young ($P_{N0} + P_{L0}$) and not vice versa. Hence variations in y impact M_{1em} and S_y (Table 6) but not M_{1im}, while variations in k_S affect M_{1im} and S_y but not M_{1em}.

Model youngsters reared locally in *L* outnumber the immigrants M_{1im}. Output values of e and S_y are about 0.5 and 0.3 respectively and vary little when S (Table 4) or G (Table 5) are altered; also $P_{N0\to4} < P_{L0\to4}$. Thus, in the illustrative model, M_{1im} comprises only 17% of P_{L0}. It is therefore possible that all surviving stream 1 youngsters return from *L* to *N* in stream 2 ($M_{1im} = 1.49 < M_{2em} = 2.88$, in P_{N1} units). An alternative scenario is that stream 2, reflecting the provenance of the population on the ground, is 17% native-reared. In this case 34% of the native-reared cocks surviving on *L* join stream 2, these comprising only 10% of the original emigrants M_{1em}. In either scenario, the illustrative model suggests that stream 2 must include some cocks reared on *L*. However, the wide *CI* for each stream (Table 7) throw doubt on this conclusion, such that stream 2 could comprise solely stream 1 returnees or none.

Age classes 3 and 4 remain in their current

Table 7. Modelled cock spring numbers and movement streams (in thousands) per 100,000 cocks (100,000 km^2 of good native Capercaillie habitat) with approximate 95% confidence intervals (*CI*). The proportion of simulations < 0 gave approximate 1-tailed probabilities that each stream did not exist (H_0 = 0 for each stream). Thus, conditional on the illustrative model and the relative population sizes that it predicts, P = 0.013 and 0.0002 for streams 1 and 2. Respective equivalents for the high survival model were P = 0.0035 and 0.0002.

Compartment	Population segment	Model			
		Illustrative*		High Survival**	
		Number	*CI*	Number	*CI*
Native	Spring cocks	100	–	100	–
Logged	Spring cocks	258	135–380	181	113–247
Migrants***	Stream 1	54	12–94	29	6–51
	Stream 2	32	13–53	17	7–28

* Illustrative model G_{N3} = 0.42, G_{L3} = 0.37.

**High survival model G_{N3} = G_{L3} = S_3 = 0.80, consistent with the western European literature (Storch 2001). Other inputs as for illustrative model.

*** Just as movement begins. For stream 1, output S_y (illustrative) = 0.30 (*CI* 0.25–0.46), S_y (high survival) = 0.21 (0.09–0.29).

compartments and suffer annual mortality (~ 0.60, Borchtchevski & Moss 2014) much higher than in the western European literature (~ 0.20, Storch 2001). Due to these losses and stream 2 emigration, they form only 16% of the population in *L* (Table 5) but, bolstered by stream 2 immigration, 52% of that in *N*. If annual mortality were ~ 0.20 the respective values would be 36% and 74%.

An alternative interpretation of the high losses borne by age classes 3 and 4 is that some cocks, failing to gain or retain lekking territories, retire to "other unlogged ground" (section 1.2.6), i.e., to a third type of compartment where they survive as well as in western or central Europe. To model this, we keep G_{N3} and G_{L3} as they are in the illustrative model but set $S_3 = 0.80$, such that the differences $S_3 - G_{N3}$ and $S_3 - G_{L3}$ are due to retirees. In this case, with $k_N = 0.5$, retiree density on the poor habitat of the third compartment would be 1.64 times as big as total cock density in good habitat, which is absurd.

3.3. Known unknowns

The model parameters mainly determining relative population and stream sizes are *G*, *S* and *y*. Each is estimated with some uncertainty or variability. Table 7 expresses the combined result of these uncertainties as *CI*, starting with a fixed number of 100,000 spring cocks in *N* (section 1.2.6). These approximate *CI*, conditional upon the relative population sizes and parameter values of the illustrative model, are for mean values and not for annual fluctuations about these means.

Further uncertainties occur when converting numbers to areas via k_d and k_N. We have insufficient information to estimate *CI* for forest areas and so characterise the effects of varying k_d and k_N by sensitivity analyses (Table 6).

3.4. Distance moved

As an example, we take the 5,000 km^2 block of native forest comprising part of the Onega-Pudoga massif within the Archangelsk region (Borchtchevski 1993), assuming $k_N = 0.5$ and $A_N = 0.25$ (25%). Apply the distance model to a disc of 5,000 km^2: the median straight-line distance moved during streams 1 or 2 is then $\sqrt{[(1 / 2 \times 0.25) + 0.5]} \times$ (radius of disc of 5,000 km^2) = 63 km.

4. Discussion

Capercaillie movements remain poorly understood. Whereas older literature describes long-distance movements including large flocks of birds (Introduction), studies of radio-tagged individuals in western and central Europe plus northern Russia (Hjeljord *et al.* 2000, Storch 2001) show a fairly sedentary pattern. Here we explore evidence for a hypothetical form of two-way movement in the largely anthropogenic forest landscape of NW Russia. The key evidence is age distributions (Table 1) that entail age-specific annual population growth rates G_{N1} and G_{N2} greater than unity (Borchtchevski & Moss 2014). These would be very unlikely in a closed population and strongly imply movement.

The model is quantitatively consistent with known facts, including vital rates of Capercaillie and the proportion of old forest remaining after logging (section 4.1.). Some parameter estimates need more study to substantiate them, as do the postulated movement streams themselves (section 4.2.) and the habitat configurations that may engender them (section 4.3.). To what extent the vast scale and intensive clear-cutting of NW Russian forest is necessary for such movements remains unclear. The model describes movements, not their ecological rationale, which we nonetheless discuss (section 4.4.).

4.1. Parameter values

Model streams 1 and 2 depend primarily on growth rates G_{L1}, G_{L2}, G_{N1}, G_{N2} and survival rates S_1, S_2. The values used for these parameters are quite well supported (Borchtchevski & Moss 2014, Storch 2001), as are those for y (section 1.2.6), G_{L3} and G_{N3} (Borchtchevski & Moss 2014). Although k_S represents a dearth of information about S_0, the sole impact of plausible variations in k_S on model movements is to vary the size of stream 1 (Table 6).

The secondary parameters k_d and k_N, which convert population sizes to areas of ground, are estimated from limited evidence. Thus k_d depends on transect-based measurements of spring density (sources cited in Borchtchevski & Moss 2014, method in Borchtchevski 1987) at three sites in native (8 site-years during 1982–2001) and four in logged forest (7 site-years during 2001–2006) and we sanguinely take their respective means to represent ~ 400,000 km^2 of NW Russian forest. Our estimate of k_N is yet more tenuous (section 1.2.6). As it stands, the density of Capercaillie in logged forest in NW Russia is sparsely documented (Borchtchevski 2011), as is the proportion of native forest that comprises good Capercaillie habitat. Although densities, and hence k_d, affect conclusions about the actual numbers of birds involved (Table 7), they have no impact on the relative numbers in each stream or compartment.

For a given set of annual growth rates G_{L1}, G_{L2}, G_{N1} and G_{N2}, the model requires specific matches between values of annual survival ($S_1 \approx S_2$) and the proportion of intact native forest (A_{N1} or A_{N2}), as observed (section 1.2.6). The absence of such matching in real-world observations would falsify the hypothesis – it survives this test but with the foregoing caveats about k_d and k_N.

4.2. Pointers for fieldwork

Movements consistent with streams 1 and 2 were not detected by the two radio-marking studies hitherto done in NW Russia (Beshkarev *et al.* 1995, Wegge *et al.* 2003, 2005, Hjeljord *et al.* 2011). Both tackled other questions, however, and involved catching cocks at leks in native forest, which would sample neither stream (Borchtchevski & Moss 2014). Studies designed specifically to detect these streams would have a better chance, but should anticipate that not all cocks join either stream. For example, in the illustrative model only about 26% of cocks of the appropriate age (P_{L1} and P_{L2}) join stream 2 (Table 5). Again, stream 1 birds returning in stream 2 may comprise only 10% or as many as 100% of the original emigrants from N (section 3.2).

Model youngsters suffer heavy overwinter mortality (Table 4 & 7), perhaps because many are killed by predators (Rykova *et al.* 2012) and hunters. Nonetheless, illustrative model output of S_y = 0.30 seems low despite few comparable estimates in the literature. In Scotland, however, Moss *et al.* (2000) found annual (September–August) survival of radio-tagged juveniles to be 0.50. If we take the value of $S_y = 0.30$ to apply to the 6 months September–February and $\sqrt{S_0}$ to cover the next 6 months, we get a juvenile annual survival rate of $0.30 \times \sqrt{0.80} = 0.27$ in NW Russia, considerably lower than in Scotland. In NW Russia, however, there are many more species of predator than in Scotland, where predator-killing is routinely practiced by gamekeepers (Summers *et al.* 2004). Moreover, if we set $y = 0.75$ and $k_S = 0.5$ then modelled juvenile survival in NW Russia becomes $0.62 \times \sqrt{0.80} = 0.55$. Clearly, the survival of juvenile Capercaillie needs further study.

A related caveat is that hen numbers P_{NB} and P_{LB}, used in calculating S_y, are estimated from $P_{N0\rightarrow4}$ and $P_{L0\rightarrow4}$ (section 1.2.3). Breeding hens, however, might be fewer than spring cocks because some hens die between spring and late summer; the adult sex ratio in spring might favour either sex; the adult sex ratio might differ between *N* and *L*; and some hens that get mated in *N* might rear their chicks in *L*, or vice versa. All these uncertainties could impact M_{1em} and hence S_y, though not M_{1im} or M_2. Plainly, hen numbers and movement need more study.

The growth rates *G* used here come from data collected in 1980–2008 and may differ when average density in the north of the Russian Plain is lower. For example, if excessive hunting leads to low adult survival (e.g., $S_{L1} \leq G_{L1}$) in logged forest, stream 2 should not occur (Borchtchevski 1993). Similarly, if stream 1 is density-dependent, it may not occur if numbers in native forest are depressed.

4.3. Distances moved

The illustrative estimate of 63 km as the median distance moved by birds shifting to and from a 5,000 km^2 block of native forest is plainly simplistic. Forest blocks are not disc-shaped, dispersal does not occur equally in all directions, and birds are not distributed randomly. Nonetheless it confirms that stream movement distances are likely to be in tens of km, consistent with Borchtchevski & Moss (2014) and with the seasonal migrations between summer and winter habitat shown by some populations in the Urals, Kazakhstan and Siberia (Introduction).

The intensive clear-cutting that created the logged forest habitat type has been associated with population declines (Storch 2001). Without logging there could be no movement between logged and unlogged habitat. Nonetheless, this may be a special case of age-related, two-way movement between poorer and better habitats. As with seasonal movements (Hjeljord *et al.* 2000), the distances involved might vary with habitat configuration at the landscape scale. Most likely, Capercaillie have an innate capacity for seasonal or age-related movement, ready to be elicited by apt natural or man-made landscapes. Certainly, more data on habitat-related densities and movements, and the causes of movement generally, are needed to test this generalisation.

4.4. Implications for population dynamics

In the model (Eq. 4), a decrease in the proportion of native forest (A_N, A_{N1} or A_{N2}) went along with a decrease in survival (S_0, S_1 and S_2). This agrees with the perception that large-scale clear-cutting is detrimental to Capercaillie (Storch 2007), although the model allows two complementary interpretations. First, with poorer survival, a bigger area of logged forest might be needed to maintain the observed age structure in a given area of native forest. Second, more logging might cause poorer survival. This might be due less to vegetation change than to the extra disturbance and hunting that follows logging in NW Russia (Novikov 1978).

Our illustrative values of S_1 and S_2 (0.80 and 0.81) are consistent with western European literature (Storch 2001), but our estimates of S_{N3} ($= G_{N3}$) and S_{L3} ($= G_{L3}$) are unprecedentedly low at ~ 0.40 (Table 5). The possibility that $S_3 > G_3$ because some subordinate cocks retire to a third compartment "other unlogged ground" cannot be completely dismissed; in the illustrative model, however, for such birds to boost S_3 to 0.80 their density in the putative third compartment would have to be greater than total cock density in *N* (section 3.2). This is highly implausible. It would, moreover, make little difference to conclusions about the existence of streams 1 and 2 (Table 7).

In the illustrative model, stream 2 involved more birds than stream 1 returnees (section 3.2, Table 5) and therefore included some reared in *L*. Indeed, the model embraces the possibility that extra cocks embark upon stream 2, but return to *L* after failing to establish themselves in *N*. Thus native forest may attract dispersing cocks independently of their provenance. On the other hand, the wide *CI*s (Table 7) make it possible that all stream 2 birds are returnees. As Capercaillie cocks do not generally attain mating status until their third spring or later (Storch 2001) streams 1 and 2 can both be classed as natal dispersal. In this case, the average natal dispersal distance of returnees could be much less than their round trip distance, and so comparable with natal dispersal distances in other Capercaillie populations. Perhaps such movements developed from the shorter movements of cocks, documented in Norway (Gjerde & Wegge 1989), whereby subadult males are displaced from lek centres by adults and retreat a few hundred m to peripheral zones between leks. In both situations, despite the different distances moved, subadults could be avoiding the more dominant adults until they are mature enough to compete at leks.

A compatible suggestion (Borchtchevski & Moss 2014) is that movements from logged to native forest are driven by a struggle for territories at big leks, accompanied by more fighting and higher mortality. The connotation that larger leks are also more attractive to females has been more studied in black grouse (*Tetrao tetrix*) than in Capercaillie. Larger black grouse leks have many more female visits and copulations, leading to a higher average male mating success (Alatalo *et al.* 1992). Also, there is evidence that female black grouse use components of fighting behaviour as cues for mate choice: a cock that fights more and has better fighting success gains more copulations (Hämäläinen *et al.* 2012). If Capercaillie are similar, stream 2 may be an adaptive behaviour pattern whereby dispersing cocks move out of logged areas and aim to establish themselves as alpha cocks at the bigger leks in native forest, so increasing their lifetime fitness despite shorter lives. Then again, they might be seeking refuge from the greater frequency of hunters in logged forest. Alternatively, stream 2 might simply comprise stream 1 emigrants returning to their natal areas once they are old enough to compete there. Well-designed studies of electronically-tagged birds could help to resolve such complementary possibilities.

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Metsokukkojen ikärakenne ja liikehdintä Luoteis-Venäjällä – kahden lokeron populaatiomalli

Luoteis-Venäjän hakkaamattomissa metsissä metsokukoilla on harvinainen ikärakenne, siten, että vanhoja lintuja on enemmän kuin nuoria. Hakatuissa metsissä vallitsee tyypillisempi, vastakohtainen tilanne. Mahdollinen selitys havaitulle ikärakenteelle on kaksisuuntainen liikehdintä, jossa nuoret siirtyvät hakkaamattomasta hakattuun metsään, kun taas vanhemmat linnut – kolmanteen kevääseen asti – liikehtivät päinvastaiseen suuntaan. Koska metsokukot eivät tyypillisesti pariudu ennen kolmatta kevättään, molemmat liikehdinnät ovat luokiteltavissa syntymälevittäytymiseksi. Kehitämme kahden lokeron populaatiomallin, joka osoittaa miten liikehdintä voi tapahtua ja teemme suurpiirteiset arviot mallin numeerisille arvioille ja etäisyyksille. Malli korostaa sitä, että tietämyksessämme on selviä aukkoja, joiden täyttäminen vaatisi lisää maastotutkimuksia.

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Appendix

Details of simulations for Table 7.

Get A_{Ni} and A_{Li} (proportion in each age class i =1–4, for N and L) and their SEs from GLM (section 2).

Define rs: for example rsA_{Ni} is a random sample from the normal distribution reconstituted from the mean and SE of A_{Ni}. For a lower case variable use parentheses e.g. $rs(x)$. Use e.g. A_{Ni} to represent the mean or central value of A_{Ni}. By default rs is from a normal distribution. In the case of S_1 use a logit expression to avoid $rsS_1 > 1$, such that logit $rsS_1 = \log_e(S_1 / (1 - S_1) + rs(x))$, where x is a number back-transformed for subsequent calculations. In the case of y, as uncertain about the mean as about the variance, use a uniform distribution for $rs(y)$. Sometimes rs is the result of an operation and constitutes a random sample from a newly-formed distribution: for example $rsA_{N0} = rsA_{N1} / rsS_1$.

Define simulated means and SE: use the SE from 10,000 rs along with the new central value from either 1) performing the same operation on the constituent means e.g., $A_{N0} = A_{N1} / S_1$ or 2) once at this stage in the calculation, the illustrative model. To get 95% CI rank 10,000 simulated rs and take those of rank 250 and 9750 as CI.

Get proportion of birds in each age class i = 0–4 (nb now includes age class 0): define $\Sigma rsA_{Ni} = rsA_{N0} + rsA_{N1} + rsA_{N2} + rsA_{N3} + rsA_{N4}$ and $rsC_{Ni} = rsA_{Ni} / \Sigma rsA_{Ni}$. From 10,000 rsC_{Ni} get seC_{Ni} (the SE of the proportion of age class i) in population N. Along the same lines we get $se\ \Sigma C_{Ni}$ where $\Sigma C_{Ni} = 1$.The same goes for seC_{Li} and $se\ \Sigma C_{Li}$.

Estimate CI for population and stream sizes in P_{N1} units using central values from the illustrative model with SE estimated as above. $P_{N0\rightarrow4}$ is fixed. The P_{N1} unit is set at mean 1 such that $P_{N0\rightarrow4} = 9.057$ (from illustrative model), but the proportion of age class 1 in N is somewhat uncertain such that $rs(P_{N1}\text{ unit}) = P_{N0\rightarrow4} \times rsA_{N1}$. $P_{L0\rightarrow4}$ is also expressed in P_{N1} units (mean 23.34 from illustrative model) and has the additional uncertainty that it is computed by adding up age classes so $rsP_{L0\rightarrow4} = P_{L0\rightarrow4} \times rs(P_{N1}\text{ unit}) \times \Sigma rsA_{Ni}$. Also $rsP_{L1} = rs\mathrm{P}_{L0\rightarrow4} \times rs\mathrm{A}_{L1}$; $rs\mathrm{G}_{L1} = rs\mathrm{A}_{L2} / rs\mathrm{A}_{L1}$; $rs\mathrm{G}_{L2} = rs\mathrm{A}_{L3} / rs\mathrm{A}_{L2}$; $rs\mathrm{G}_{N1} = rs\mathrm{A}_{N2} / rs\mathrm{A}_{N1}$. This provides SE for the calculations of the CI for stream sizes from the illustrative model:

$rs(e) = (rsP_{L1} \times ((P_{N0\rightarrow4} / (P_{N0\rightarrow4} + rsP_{L0\rightarrow4})) \times (P_{N0\rightarrow4} + rsP_{L0\rightarrow4})) - ((rsP_{L0\rightarrow4} / (P_{N0\rightarrow4} + rsP_{L0\rightarrow4})) \times (P_{N0\rightarrow4} + rsP_{L0\rightarrow4}))$
$\times (1 + rsP_{L1}))$,
$rsM_{1em} = rs(e) \times P_{N0\rightarrow4} \times rs(y)$,
$rsM_{2em} = (rsG_{N1} - rsS_1) + (rsP_{L1} \times rsG_{L1} \times (rsS_2 - rsG_{L2}) / rsS_2)$.

Repeat simulations 10,000 times and take CI. Convert all results to $P_{N0\rightarrow4}$ = 100,000 by × 100,000 / 9.057.