Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals

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Abstract: The rate of adaptive evolution, the contribution of selection to genetic changes that increase mean fitness, is determined by the additive genetic variance in individual relative fitness. To date, there are few robust estimates of this parameter for natural populations, and it is therefore unclear whether adaptive evolution can play a meaningful role in short-term population dynamics. We applied new quantitative genetic methods to long-term datasets from 19 wild bird and mammal populations, and found that, while estimates vary between populations, additive genetic variance in relative fitness is often substantial, and on average double previous estimates. We show that these rates of contemporary adaptive evolution can impact population dynamics, and hence that natural selection has the potential to partly mitigate effects of current environmental change.

One-Sentence Summary: Genetic variance in fitness in 19 wild vertebrate populations suggests adaptive evolution is currently common and rapid.

Main Text:

How fast are wild populations currently evolving in response to natural selection? The rate of adaptive evolution in nature is both of fundamental theoretical importance, and also of increasing practical relevance given the clear impact of human activities on the environment experienced by wild organisms (*1*). There are numerous examples of phenotypic and genetic changes for traits under selection (*2-5*), which suggests that adaptive evolution can occur in wild populations over contemporary timescales. At the same time, however, many studies have found that trait changes do not correspond to adaptive expectations or suggest evolutionary stasis (*6, 7*). However, estimates of the rate of evolution of specific traits are unlikely to represent the overall rate of adaptation of a population, as natural selection acts on many traits concurrently. Instead, a comprehensive assessment of the rate of adaptive evolution in a population needs to integrate adaptive genetic changes across all traits that determine individual fitness, i.e. the contribution of an individual to the gene pool of the next generation.

According to Fisher's Fundamental Theorem of Natural Selection, the per-generation proportional change in mean absolute fitness caused by natural selection is given by the additive genetic variance in relative fitness, $V_A(w)$ (*8-10*). In non-technical terms, $V_A(w)$ is the extent of heritable (transmitted from parents to offspring) genetic differences in the ability to reproduce. The realized change in mean fitness between generations may deviate from $V_A(w)$ because of concurrent effects of genetic mutations, gene-flow, environmental change or gene-environment interactions (*8, 9, 11*). Nonetheless, a non-zero value of $V_A(w)$ indicates that, all else being equal, natural selection contributes to an increase in mean fitness (*8, 9*). It also indicates that at least some of the traits that determine individual fitness are currently evolving in response to

selection. Thus, $V_A(w)$ is arguably the most important evolutionary parameter in any population (*9, 12*).

Robust estimation of $V_A(w)$ requires accurate measures both of individual fitness and pairwise genetic relatedness for large numbers of individuals. Such data are difficult to collect for wild populations of animals or plants (*13*). Moreover, their analysis is made challenging by the distribution of individual fitness, which generally does not conform well to common statistical methods (*14*). Consequently, our knowledge of $V_A(w)$ in natural populations is currently limited: two reviews report estimates of $V_A(w)$ from 16 populations of 13 plant and (non-human) animal species with fitness measured over complete lifetimes (*12, 14;* we discuss these results alongside our own below). However, notwithstanding possible issues specific to each analysis (such as the omission of important non-genetic sources of similarity between relatives), most of these estimates were obtained from Gaussian models (for exceptions see *10*) which generally do not fit the distribution of fitness well. In natural populations, the distribution of fitness of all individuals is typically both highly right-skewed, with most individuals having low values but a few having very high values, and zero-inflated, with an excess of zeroes over and above that otherwise expected (zero-inflation may for example be generated by high levels of juvenile mortality). Estimates of $V_A(w)$ from Gaussian models, and their associated uncertainty, may thus be unreliable (*14, 15*).

Here, we address the gap in our knowledge of the value of $V_A(w)$ in the wild and its implications in terms of adaptation, trait evolution and population dynamics. We apply new Bayesian quantitative genetic methods to data from long-term studies of 19 free-living vertebrate populations with high-quality lifetime reproduction and multi-generational relatedness data. Covering more populations and species than all previous studies combined, these 19 populations of 15 different species (6 birds and 9 mammals) have contrasting ecologies, life histories and

social systems (*10,* SI Table S1-2) and are located in diverse terrestrial biomes and continents (Fig. 1). Our analysis is restricted to birds and mammals because of their predominance among long-term studies with suitable data (*13*). The populations have been monitored for between 11 and 63 years, providing fitness records for 561 fully monitored cohorts totaling 249,430 individuals of both sexes (*10*). For all data-sets used here, an individual's fitness was measured as 'lifetime breeding success', the total number of offspring produced over its lifetime, irrespective of offspring survival. While there are numerous definitions of fitness, each motivated by different theoretical frameworks (*16*), measuring fitness as lifetime breeding success corresponds most closely to a life-cycle-calibrated 'zygote-to-zygote' definition of individual fitness, consistent with quantitative genetic theory (*17*). Individuals were identified soon after birth or hatching, and fitness was estimated for all known individuals in each population, including the, often large, proportion that died as juveniles (*10*). We modeled absolute lifetime breeding success using a quantitative genetic form of mixed effects model known as an 'animal model' (*18*), assuming that lifetime breeding success follows zero-inflated over-dispersed Poisson distributions and including relevant covariates (such as inbreeding, genetic group, sex and cohort. See *10,* Table S3-4, Text S1 for model details, Fig. S1-2 for evaluation of model goodness of fit, Text S2, Fig. S3 for prior distribution). The zero-inflated Poisson models were fitted to absolute fitness data and the resulting parameter estimates, obtained on link-function scales, were then back-transformed to derive estimates of $V_A(w)$ and other components of variances for relative fitness on the scale of the data (*15*). We first ran one model for each study population, and subsequently combined results into a meta-analysis (*10).*

We found evidence for additive genetic variance in relative fitness in multiple populations. Our models provided estimates of $V_A(w)$ with posterior modes ranging from 0.003 to 0.497 (Fig 2A). The 95% credible intervals (95%CI) for $V_A(w)$ excluded values below 0.001 in ten of the 19

populations, and excluded values below 0.01 in eight (thresholds explained in caption of Fig. 2A, Text S2, S3). Therefore, there was clear evidence that selection contributed to genetic changes, and hence a predicted increase in fitness, in roughly half of the study populations (*9, 19*). Across populations, the median of the posterior modes for $V_A(w)$ was 0.100 and the meta-analytic mean of $V_A(w)$ was 0.185, 95%CI [0.088; 0.303]. There was also considerable variation among populations, with a meta-analytic among-population standard deviation in $V_A(w)$ of 0.11, 95%CI [0.01; 0.26]. The median and mean values of $V_A(w)$ were about four and two times larger than those of previous estimates (previous median 0.023; previous mean 0.092; *12, 14*). Our values can be considered large given theoretical considerations (SI Text S3, Fig. S4), and they were robust to the modeling of possible confounders: inbreeding, sex, linear environmental changes in mean fitness, gene-flow due to immigration, variance among cohorts and among mothers (*10)* and also mother-by-cohort interactions, social group effects (SI Text S4, Table S5, Fig. S5) and the social inheritance of social dominance within families (SI Text S5, Fig. S6-7). For completeness, we also present estimates relating to an alternative formulation of Fisher's Fundamental Theorem expressing change in terms of absolute fitness leading to the same conclusions (Text S6, Fig. S8).

Previous work on adaptive evolution has often focused on the heritability of fitness, $h^2(w) = V_A(w)/V_P(w)$, where $V_P(w)$ is the phenotypic variance in relative fitness, or 'opportunity for selection' (*20*). However, $h^2(w)$ may be a poor measure of the overall rate of adaptive evolution (*20*). In natural conditions, stochastic or unaccounted environmental variation is expected to dominate variation in individual fitness, even in the presence of large deterministic sources of variation in fitness (*21*), so that $h^2(w)$ may be small even when $V_A(w)$ is large (*21, 22*). In line with this expectation, we found that $h^2(w)$ was generally small, with a meta-analytic average of 2.99%, 95%CI [0.80; 6.60%] and a value of less than 1% in 11 populations (Fig. 2B), similar to

previous estimates of $h^2(w)$ (*14*). Nevertheless, estimates of $h^2(w)$ were of similar magnitude to the proportion of variance explained by maternal effect and cohort variances (Fig. 2B, SI Text S7, Table S6-10 for parameter estimates on different scales). Furthermore, $h^2(w)$ was highly variable between populations and was sometimes substantial, with posterior modes ranging from 0.019% to 17.1%.

What do our estimates of $V_A(w)$ imply about the evolution of traits in our study populations? $V_A(w)$ is the partial increase in fitness expected to result from the combined responses to selection across heritable traits (*23*). Therefore, a non-zero $V_A(w)$, as was found for at least half of our study populations, implies that for one or several traits, the responses to selection tend to cause adaptive change, although the total change may be affected by mutations or environmental change (*19*). The value of $V_A(w)$ sets an upper bound for the possible per-generation response to selection of any trait (*19*). Given the meta-analytic estimate of $V_A(w)=0.185$, and a trait with a heritability of 0.3 (an average value for trait heritability in wild populations, *24*), the maximal rate of response to selection is 0.24 standard deviations per generation (*10, 19*). Across our 19 populations, the upper bound of response to selection for a trait with a heritability of 0.30 varies from 0.05, 95%CI [0.01;0.13], to 0.39, 95%CI [0.29;0.50] standard deviations. These upper bounds are substantial: for comparison, in natural populations the rates of phenotypic change, irrespective of whether the change is known to be adaptive, are rarely above 0.03 standard deviations (around 10% of estimates), and only very rarely above 0.13 standard deviations (around 5% of estimates; *2*). Furthermore, evolutionary studies of wild populations, including several conducted in our study populations, have often failed to detect phenotypic change in response to current selection (*5, 6, 25*). Our results may therefore appear at odds with these observations. However, attempts to estimate genetic evolution of traits, as opposed to just phenotypic trends, remain rare and under-powered (*25*). Genetic evolution of traits may be

masked at the phenotypic level, either because phenotypic plasticity hides genetic change (*6*) or because direct evolution is counterbalanced by the evolution of 'indirect genetic effects', that is, the effect of other individuals' genotypes (*26*). Moreover, approaches to estimating genetic change for a trait, such as estimation of trends in individual genetic merit ('breeding values') (*27*) or by estimation of polygenic scores (*28*), may have limited statistical power. Finally, if $V_A(w)$ is ultimately driven by the cumulative effects of many traits evolving in response to selection, the evolutionary change in each trait will be small and even more difficult to identify statistically. Any or all of these scenarios could prevent observed rates of phenotypic change in single traits reaching the upper bound of what might be possible given the observed levels of $V_A(w)$.

Irrespective of the rates of adaptive evolution in the potentially many traits that contribute to $V_A(w)$, our estimates of their combined effect, summarized in $V_A(w)$, indicate that adaptive evolution may have substantially affected recent population dynamics (see Text S6, S8, Fig. S8). For instance, in a thought experiment assuming that no forces oppose adaptive evolution and that $V_A(w)$ remains constant, 11 out of our 19 populations would recover from an arbitrary one-third reduction in fitness in fewer than 10 generations (SI Text S8). Moreover, the median $V_A(w)$ of 0.10 means that in half the populations, natural selection tends to increase mean absolute fitness by at least 10% every generation. While such a change would lead to exponential population growth if not counterbalanced, none of our study populations showed any exponential increase in population size such as predicted by the thought experiment (SI Text S9). This indicates that any adaptive evolution was countered by simultaneous deleterious effects of other processes such as mutation, gene-flow, or environmental changes (*19*). The presence of these counterbalancing forces, as well as potential changes in future selective pressures and the potential instability of $V_A(w)$ in future environments, make it impossible to project whether the contemporary adaptive

evolution that our results indicate is sufficiently fast and lasting to ensure population persistence. Other studies that focused on specific traits, rather than on the net effect of selection on fitness, suggest that short-term phenotypic changes in response to climate change are overall insufficient to ensure the persistence of populations (*29, 30*). Crucially, however, our finding that most populations harbor biologically meaningful levels of additive genetic variance in fitness indicates that the machinery of adaptive evolution often operates at a substantial pace on generation-to-generation timescales. Without ongoing adaptive genetic changes, these populations would presumably have had, often substantially, lower growth rates over recent generations.

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Methodology: TB, MBM, PdV, LEBK

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Supplementary Materials

Materials and Methods

Supplementary Text S1 to S10

Figs. S1 to S10

Tables S1 to S10

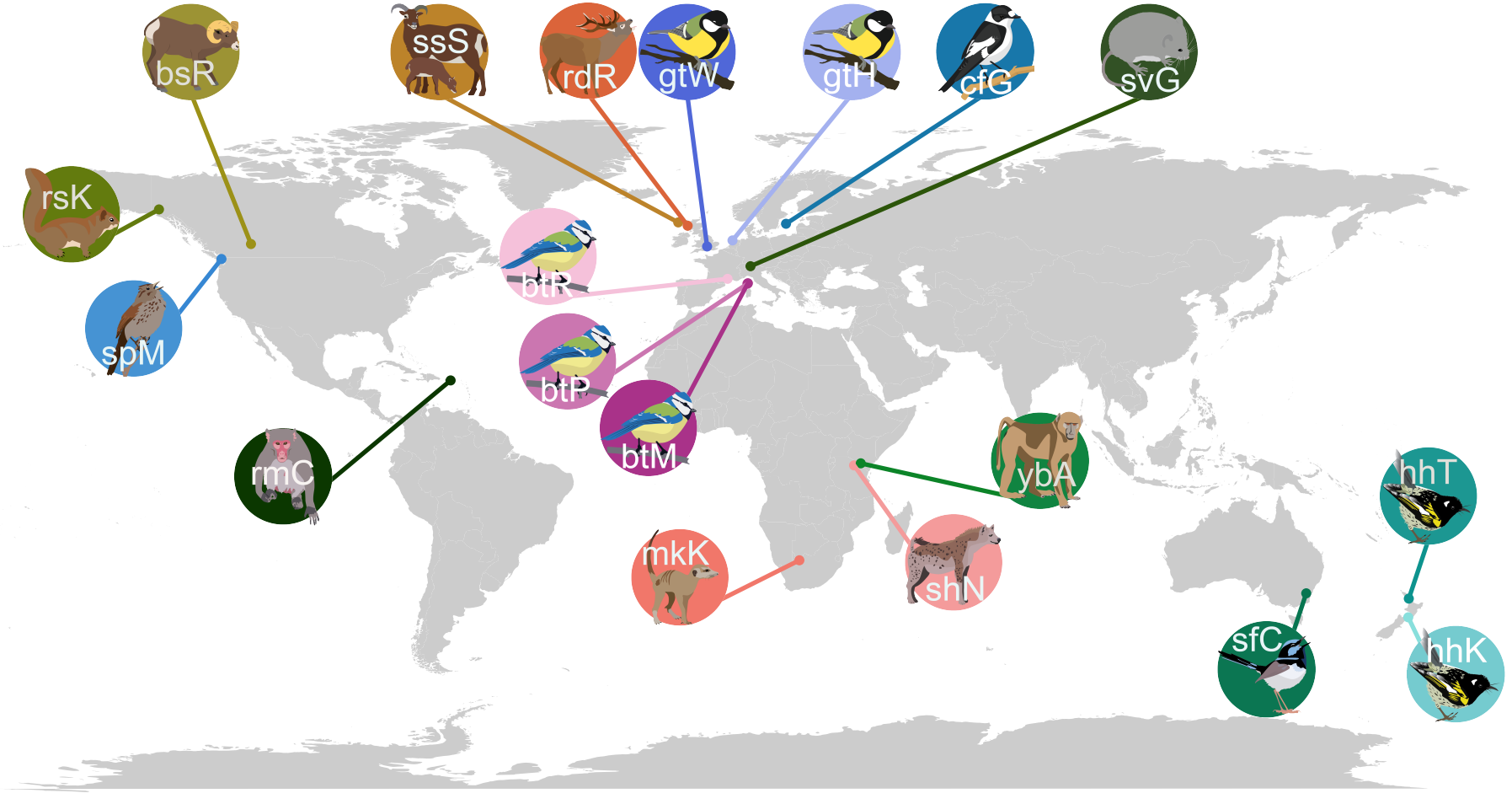
References (*31–242*)

Data S1

Code S1

Fig. 1. Locations of the 19 long-term population studies. From top to bottom and then left to right: bsR = bighorn sheep on Ram Mountain, ssS = Soay sheep on St Kilda, rdR = red deer on the Isle of Rum, gtW = great tits in Wytham Woods, gtH = great tits in Hoge Veluwe, cfG = collared flycatchers on Gotland, svG = snow voles in Graubünden, rsK=red squirrels in Kluane, btR = blue tits at la Rouvière, spM= song sparrows on Mandarte Island, btP = blue tits at Pirio, btM = blue tits at Muro, rmC = rhesus macaques at Cayo Santiago, ybA = yellow baboons at Amboseli, hhT = hihi on Tiritiri Matangi Island, shN = spotted hyenas in the Ngorongoro Crater, mkK = meerkats in the Kalahari, sfC = superb fairy-wrens in Canberra, hhK = hihi at Karori.

Fig. 2. Additive genetic variance and other components of variance in relative fitness. Panels show posterior distributions of each parameter: (**A**) additive genetic variance in relative fitness, $V_A(w)$; (**B**) proportion of phenotypic variance in fitness due to different variance components: additive genetic variance, i.e., heritability (red), maternal effect variance (light blue), cohort variance (dark green). Species are ordered by phylogenetic proximity. Each distribution has an area of 1 but is scaled arbitrarily on the y-axis to aid comparison. Asterisks: * indicates that the 95%CI of a variance component does not overlap 0.001 (approximately the mode of the prior distribution for $V_A(w)$, Text S2); ** that the 95%CI does not overlap 0.01 (the approximate threshold between small and moderate rates of adaptive evolution, Text S3); asterisks indicate absolute variance values, not proportions of variance. See Fig. 1 caption for full population names.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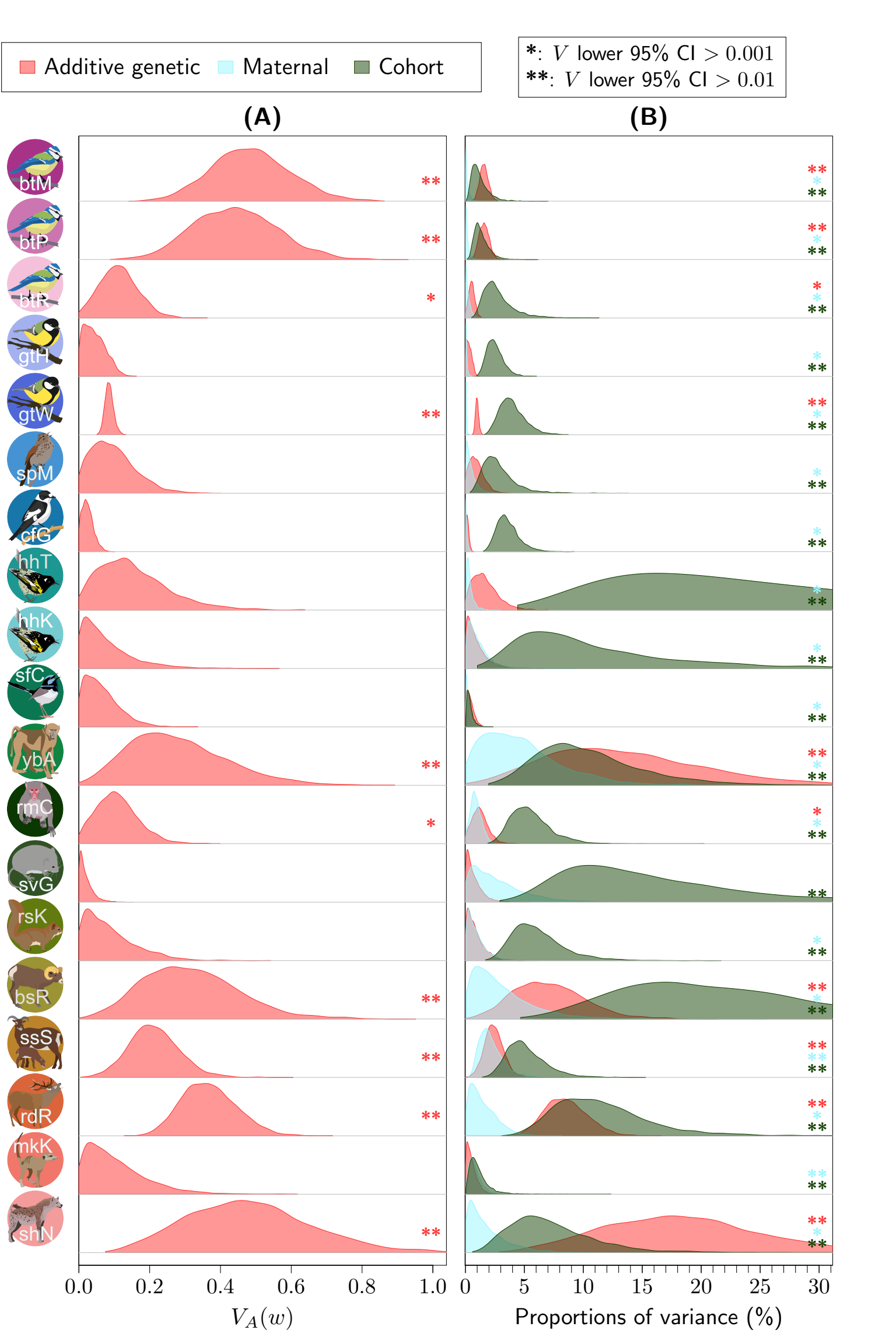
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$V_A(w)$
0
5
10
15
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25
30
Proportions of variance (%)

Science
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Supplementary Materials for

Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals

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Materials and Methods

Short summary of the Methods

Data collection

We assembled data sets from the long-term monitoring of 19 pedigreed wild bird and mammal populations with individual fitness known over multiple generations, as described below. Parent-offspring relationships were reconstructed from genetic data and field observations (details of each population below). These were then used to infer both lifetime breeding success, defined as the total number of offspring produced by an individual across its lifetime, for all marked or otherwise identified individuals (including those who were marked but then died as juveniles), and pairwise genetic relatedness between all individuals (constructed from multi-generational pedigrees, for use in the quantitative genetic analyses). Inevitably, as for any field study, lifetime breeding success may not be measured perfectly for all individuals, and in particular may be underestimated because some individuals die or emigrate before ever being captured. However our data selection focused on individuals with the best life history information in each population. As in all studies of fitness in natural populations, our analysis therefore assumes that individuals are missing at random with respect to their genetic value for LBS (*31*).

Estimation of additive genetic variance in relative fitness

We estimated quantitative genetic parameters using 'animal models' (*18, 32*) assuming lifetime breeding success represents absolute fitness (written W) and follows a zero-inflated over-dispersed Poisson distribution. Zero-inflated models have two parts: a 'zero-inflation component' and a 'conditional-Poisson component', each consisting of a linear combination of parameters on a transformed link scale (see below for further details). Parameters estimated on the two link scales of the linear predictors for absolute fitness were back-transformed to the data scale using the framework outlined in (*33–35*), to obtain parameters relevant for relative fitness (written w, with $w = W/\bar{W}$, $\bar{W}$ being mean absolute fitness) on the data scale, in particular the additive genetic variance in relative fitness $V_A(w)$. In addition to additive genetic random effects, all models also contained random effects of maternal identity and year of birth ('cohort'), and additional random effects to account for social structure in populations where they are known to be important (identity of social groups in the rhesus macaque, meerkat and spotted hyena populations, and litter identity in the meerkats). We explicitly estimated the covariance between the zero-inflation and conditional-Poisson components for each random effect. Also, all models contained a residual dispersion random effect, with a variance estimated for the Poisson component, a variance fixed to 1 for the zero-inflation component, and a covariance between the two components fixed to 0.

For both the zero-inflation and the conditional-Poisson components, we fitted fixed effects of an individual's inbreeding coefficient (estimated from the pedigree), expected proportion of immigrant genetic ancestry ('genetic group', (*36*)), sex and cohort (year of birth, as a linear covariate). Fitting cohort as a linear covariate allowed us to

correct for potential biases in the estimation of breeding values if mean fitness changes through time in response to some change in the environment (*37*)). Furthermore, for social species (yellow baboons, rhesus macaques, meerkats and spotted hyenas), we incorporated a measure of social dominance rank. For each study population, we report results from the full (i.e. incorporating all variables, and so probably most conservative) model in the main text, but also present models with simpler fixed and random effect structures in supplementary text S4. In general, we found that the fixed and random effects had little influence on the estimation of $V_A(w)$ within each population, and virtually no influence on summary statistics and meta-analytic estimates across populations. Each population was first analysed with its own model, with both sexes analysed together. Models were fitted in the Bayesian R-package MCMCglmm (*38*) and uncertainty in each parameter was propagated to derived parameters by integrating over the full posterior distribution.

Data selection and formatting

We used data from 19 long-term individual-based studies of pedigreed wild animal populations (Tables S1 and S2), for which measures of individual fitness were available for multiple generations. We excluded human populations because they may arguably not be regarded as wild, although some do constitute good examples of contemporary evolution (*26, 39*).

Table S1: Population location, study species, range of cohorts (years of birth) included in the analyses, number of cohorts, number of individuals with complete lifetime breeding success data ('LBS'), and number of individuals with known sex ('Sex') .

Population location	Species	Scientific name	Class	Cohorts	Number	LBS	Sex
Muro, Corsica, France	Blue tit	*Cyanistes caeruleus*, Linnaeus 1758	Birds	1993 - 2016	24	13505	606
Pirio, Corsica, France				1976 - 2016	41	9672	492
la Rouvière, Occitanie, France				1991 - 2016	26	13891	917
Hoge Veluwe, Gelderland, the Netherlands	Great tit	*Parus major*, Linnaeus 1758		1955 - 2011	57	59999	26640
Wytham Woods, England, United Kingdom				1964 - 2016	53	83546	13680
Mandarte Island, British Columbia, Canada	Song sprarrow	*Melospiza melodia*, Wilson 1810		1993 - 2012	20	2821	2821
Gotland, Sweden	Collared flycatcher	*Ficedula albicollis*, Temminck 1815		1980 - 2011	32	35385	5025
Tiritiri Matangi, Auckland, Aotearoa New Zealand	Hihi (Stitchbird)	*Notiomystis cincta*, Du Bus 1839		1995 - 2015	20	2327	2089
Karori, Wellington, Aotearoa New Zealand				2004 - 2016	13	1011	832
Canberra, ACT, Australia	Superb fairy-wren	*Malurus cyaneus*, Ellis 1782		1988 - 2012	25	7198	6901
Amboseli, Kenya	Yellow baboon	*Papio cynocephalus*, Linnaeus, 1766	Mammals	1959 - 2004	46	771	771
Cayo Santiago, Puerto Rico	Rhesus macaque	*Macaca mulatta*, Zimmermann, 1780		1970 - 2002	33	4219	4219
Churwalden, Graubünden, Switzerland	Snow vole	*Chionomys nivalis*, Martin 1842		2005 - 2015	11	1064	1064
Kluane, Yukon, Canada	Red squirrel	*Tamiasciurus hudsonicus*, Erxleben 1777		1989 - 2009	21	2680	2680
Ram Mountain, Alberta, Canada	Bighorn sheep	*Ovis canadensis*, Shaw 1804		1975 - 2005	31	820	820
St Kilda, NW Scotland, United Kingdom	Soay sheep	*Ovis aries*, Linnaeus 1758		1985 - 2008	24	4190	4190
Isle of Rum, NW Scotland, United Kingdom	Red deer	*Cervus elaphus*, Linnaeus 1758		1956 - 2001	46	2922	2922
Kalahari, Northern Cape, South Africa	Meerkat	*Suricata suricatta*, Desmarest 1804		1993 - 2015	23	2601	2601
Ngorongoro Crater, Tanzania	Spotted hyena	*Crocuta crocuta*, Erxleben 1777		1992 - 2005	14	756	756

We restricted our analyses to studies with substantial length, sample sizes and pedigree depth (Table S2), and for which relatedness information has already been used for quantitative genetic analyses, to ensure that the complex and data-demanding models fitted here had a chance to be estimable. We are aware of the limited taxonomic diversity and representativeness of the collection of studies here, and hope that the approach can be applied to a wider range of taxa in the future.

For each population, we restricted analysis to data on individuals from successive cohorts in which at least 95% of known individuals were already dead, to ensure accurate measures of lifetime breeding success for a given cohort. In total, the datasets summed to 561 cohorts containing the fitness records of 249,430 individuals (Table S1).

Table S2: Pedigree information for each study population.

Population	Individuals	Maternal Links	Paternal Links	Full-sibships	Half-sibships	Depth mean/max
Blue tit Muro	15545	13505	13505	53382	87856	1.88 / 9
Blue tit Pirio	11314	9672	9672	33027	62989	1.87 / 16
Blue tit la Rouvière	15235	13891	13891	68993	111753	4.18 / 15
Great tit Hoge Veluwe	70549	53248	53248	269916	441130	2.39 / 21
Great tit Wytham Woods	86104	77295	77295	334703	436103	8.09 / 38
Song sparrow Mandarte	3062	3010	3010	8448	35633	16.63 / 26
Collared flycatcher Gotland	42975	35496	35496	77510	174556	2.47 / 16
Hihi Karori	1120	988	667	583	7389	4.04 / 10
Hihi Tiritiri Matangi	2620	2504	1759	1872	26680	6.68 / 13
Superb fairy-wren Canberra	9964	8241	7357	14919	106796	3.83 / 15
Yellow baboon Amboseli	1587	1330	610	114	5230	3.1 / 8
Rhesus macaques Cayo Santiago	4403	1897	1840	125	16987	1.19 / 6
Snow vole Graubünden	1135	883	896	508	3375	3.63 / 12
Red squirrel Kluane	4454	4057	647	374	21693	2.49 / 8
Bighorn sheep Ram mountain	1169	898	558	45	4191	2.65 / 9
Soay sheep St Kilda	4964	4185	3766	273	39554	4.39 / 12
Red deer Isle of Rum	2990	2459	1621	162	16128	2.88 / 9
Meerkat Kalahari	3309	2981	2243	14102	37445	4.09 / 10
Spotted hyena Ngorongoro	880	736	474	245	3625	1.63 / 4

Notes: Individuals shows the number of focal individual in the pedigree, with Maternal, Paternal, Full-Sibships and Half-Sibships indicating the number of the respective pedigree links. Half-sibships are counted excluding full-sibships. Depth indicates the mean longest path leading to each individual in the pedigree, together with the maximum value in the dataset. Pedigrees were pruned to include only links that contain information about relatedness for phenotyped individuals.

Details of population monitoring and data selection for each population

Below we provide brief descriptions of each population's monitoring, and references to more detailed information for each. Species are ordered in the same taxonomic order as in tables and figures.

Blue tits (*Cyanistes caeruleus*): la Rouvière, Montpellier and Muro and Pirio, Corsica, France

The Blue tit (*Cyanistes caeruleus*) is a small passerine (body mass ca. 9.5-11.5g), common in the west Palearctic, inhabiting a large range of ecosystems such as forests, agricultural areas, gardens and parks in the countryside as well as cities. It is insectivorous during spring and has a diversified diet including seeds and berries outside the breeding season. A long-term monitoring of blue tit populations in the South of France (mainland and Corsica) was initiated in 1976 (*40*). Birds in Corsica belong to the subspecies *C. c. ogliastrae* and are around 15% smaller than mainland birds. In this study, we used data collected in three study sites (one mainland, two on Corsica) where more than 1000 nest-boxes have been erected, allowing close monitoring of all broods and breeding birds during each breeding season. The study locations are in forests of either deciduous (*Quercus pubescens*) or evergreen (*Quercus ilex*) oaks. Research over more than 40 years has revealed that blue tits from these two types of forest differ in many traits, including their morphology, life-history, behaviour, physiology and colour (*40, 41*). The dataset in this analysis includes reproductive events up until 2017, with the following dates for the first year of monitoring: 1976 for Pirio (evergreen site in the Fango valley in Corsica), 1991 for Rouvière (deciduous forest close to Montpellier in mainland France) and 1993 for Muro (3 deciduous and 3 evergreen patches of forest in the Regino valley in Corsica).

A blue tit breeding event starts with the building of the nest by both the male and the female. The female lays a clutch that can range from 5 to 15 eggs depending on environmental conditions and populations. After the entire clutch is laid, the female incubates the eggs for 14 days. From hatching until fledging at around 21 days, parents feed the nestlings mainly with caterpillars, but also with other prey such as spiders (*42*). It is estimated that one nestling requires around 1800 caterpillars during its development (*42, 43*). Synchronisation between the caterpillar peak date of abundance and nestling development is thus a crucial determinant of reproductive success (*44, 45*).

During each breeding season, all bird pairs laying in nest-boxes are monitored at least weekly. Note that birds are free-living but all breeding events are monitored in are human-made concrete nest-boxes, which may affect the means and variances in birds' phenotypes (*46*). Every week, each nest-box is checked to record laying date, clutch size, number of nestlings and number of fledglings for all breeding attempts. In addition to phenological and reproductive success data, all breeding parents are captured when feeding their 10-15 days old nestlings, ringed and measured for their morphology (tarsus length, body mass, wing length, beak length) and docility (*47*). Nestlings are also ringed and measured (tarsus length and body mass) at day 14 or 15. This monitoring enables production of pedigrees for quantitative genetic analyses based on social information (i.e. with parentage determined by observation of the identity of the parents attending a nest). Previous studies show relatively high extra-pair paternity rates in these populations (16-25% of young are sired by an extra-pair male, (*48*)), which are positively correlated with population

density (*49*). Additive genetic variance may hence be underestimated since analyses are based on largely social rather genetic pedigrees, with an underestimation expected to be below 15% ((*50, 51*); (*52*)). However use of the 'social' pedigree was required because genetically-determined pedigrees are not available for the large majority of cohorts considered here.

Captures were performed under personal ringing permits delivered by the CRBPO (Centre de Recherches par le Baguage des Populations d'Oiseaux, e.g. ringing permit for Anne Charmantier was number 1907) for the Research Ringing Programme number 369. All experimental protocols were approved by the Ethics Committee for Animal Experimentation of Languedoc Roussillon (CEEA-LR, most recent approval on 05/06/2018) as well as by Regional Institutions (by-law issued by the Prefecture de la Haute Corse number 2015-491 on 08/12/2015).

Great tits (*Parus major*): Wytham Woods, England

Great tits are hole-nesting passerine birds weighing approximately 16-20g (males are c. 5% heavier than females), and are found across much of Europe and Asia. They readily adopt nestboxes as nesting sites, making it relatively simple to observe breeding behaviour and to census populations, and hence they are a popular choice for studies of wild populations.

Wytham Woods is an area of mature, mixed deciduous tree species covering 385 hectares. Monitoring of the breeding population of great tits in Wytham Woods began in 1947, and by the early 1960s had expanded across the full 385-hectare site, with a total of 1020 nestboxes, since when the number and position of nestboxes has been fixed. Breeding records used in the present study span 1964-2016 (i.e., 53 years). Analyses indicate that a large majority of the breeding population uses nestboxes as nesting sites (*53–55*). As described in detail elsewhere (*56*), beginning in late March, nestboxes are visited regularly to look for signs of nest-building, to count eggs, and to check for hatching and fledging success. Nestlings are fitted with uniquely numbered leg-rings when two weeks old (i.e., prior to fledging), as are any previously uncaught adults (i.e., presumed immigrants), allowing individuals to be identified upon recapture and the population pedigree to be extended. Historically, adults are caught at the nestbox during chick-feeding but more recently RFID tagging of birds has allowed some parents to be identified without capture, either while incubating/brooding (females) or when entering/leaving the nestbox (both sexes). Provisioning adults are presumed to be the biological parents of the chicks in the nest (resulting in construction of a 'social pedigree'), although extra-paternity does occur (c. 13-14% of offspring are sired by an extra-pair male; (*57, 58*)). Extra-pair paternity creates errors in the population pedigree and, in the case of fitness estimates, in the phenotypes of interest. Pedigree errors of this size are typically expected to have a limited quantitative effect on quantitative genetic analyses of traits (*50, 59*), but in this case the bias they introduce to the phenotypic scores of males' LBS means we cannot be certain of the impact of EPP on results. LBS was defined as the number of fledged offspring raised by each known fledgling. The population is relatively open, such that approximately 49% of known breeders are immigrants (*60*); conversely, an unknown proportion of fledglings will settle and breed

outside the study area. However, typical dispersal distances within the study site are small (median dispersal distance for females: 771m; males: 532m; (*61*)), and much of the surrounding area is open farmland, so we assume estimates based on local recruitment to be indicative of global recruitment. A website is dedicated to presenting the monitoring: http://wythamtits.com/.

Ethical approval for the study was granted by the British Trust for Ornithology and Oxford University's Department of Zoology Ethical Review.

A previous study of the heritable variation of fitness in this population defined lifetime reproductive success as the total number of recruited offspring produced per observed first-year breeder, with female and male Lifetime Recruitment Success (that is the number of recruits produced by every recruit) modelled separately using REML-based animal models with Gaussian distributions (*55*). These models differed from the current analyses in fitting small-scale (i.e., nestbox-level) spatial heterogeneity as a random effect and treating the cohort as a multi-level factor fixed effect. Additive genetic variances ($\pm$ standard error) for absolute lifetime number of recruits (which is a worse measure of fitness than LBS in a quantitative genetic framework) were estimated as 0.004 ± 0.078 for females and 0.031 ± 0.072 for males.

Great tits (*Parus major*): Hoge Veluwe, the Netherlands

In the Hoge Veluwe area, great tits lay clutches of typically between 6 and 12 eggs. After a clutch fails they may produce a replacement clutch. In some years, second broods are produced, varying from 5% - 80% (*62*). Birds may already reproduce in the first year after fledging. About 10% of the fledglings return to breed in the study population (recruit), and annual adult survival is about 50%; both these values depend on winter conditions (*63*).

The Hoge Veluwe population has been monitored since 1955 and is located in the National Park de Hoge Veluwe. There are about 400 nest boxes with an entrance hole suitable for great tits and 50 selective boxes that can be used by blue tits only. A severe storm in the winter of 1972-1973 required a restructuring of the nest box area and therefore the 1955-1972 period is sometimes referred to as HV1, and the period starting in 1973 as HV2 (*64*). The area consists of a mix of deciduous and evergreen tree species on a sandy soil. Next boxes are checked weekly from April to July to determine laying date, clutch size, brood size, hatching date and fledging date. All chicks are ringed and almost all parents ($> 90\%$) are caught and identified by their ring. Since 1992, parents have been blood sampled for DNA, and since 2005 all chicks have also been blood sampled (with a part of the population sampled in the years before). Caterpillar biomass abundance is measured twice a week (*45*) and beech crop is also measured (*63*). The research is currently done with a licence of the Centrale Commissie Dierproeven (CDD) under number AVD801002017831.

Song sparrows (*Melospiza melodia*): Mandarte island, Canada

Song sparrows are passerine birds (typical body mass ∼25g) that are widely distributed across North America (24 recognised subspecies, (*65*)). The species is phenotypically monomorphic and primarily socially monogamous; females and males defend territories and contribute to care for dependent offspring. Social pairings can typically rear up to three broods of up to four offspring per year, with substantial variation among individuals and years (*65–67*). However social polygyny and polyandry occur (*68*), and there is regular divorce and repairing (*69*) and substantial extra-pair reproduction. Specifically, in the focal population, ca. 28% of offspring were sired by local extra-pair males, affecting 44% of observed broods (*70*). Female and male reproductive success can consequently differ substantially across years and lifetimes despite the predominant social monogamy (*71*). Mean survival from hatching to adulthood at age one year is 0.17 for females and 0.21 for males (*67*), but varies substantially among years (*65*). Mean adult lifespan is 2.1 years for females and 2.3 years for males (*67*), and the mean generation time is ∼2.5 years (*72*).

The focal population on Mandarte island, British Columbia, Canada (48°38′N, 123°17′W, 6 hectares) has been studied intensively since 1975. The work has taken place under University of British Columbia Animal Care Committee certification (held by Prof. Peter Arcese), and with permission of the Tsawout and Tseycum First Nations. The population inhabits an area of natural scrub and adjoining grassland. Each year since 1975, all territories and nests have been closely monitored, all chicks surviving to ca. six days post-hatch have been marked with unique colour-ring combinations, all surviving adults have been identified, and the occasional adult immigrant (ca. 1/year on average) have also been caught and colour-ringed (*66, 67*). Since 1993, small blood samples were collected from all ringed individuals under licence. All individuals were genotyped at up to 160 polymorphic microsatellite markers, allowing their true genetic parents to be identified with extremely high individual-level statistical confidence (*70, 73, 74*). A comprehensive, genetically-verified pedigree was then constructed for 1993–2016 (*75*), using the R package MasterBayes (*76*). The resulting data allows accurate quantification of individual fitness metrics, and also of the inverse relatedness matrix required for quantitative genetic animal model analyses (*67, 75*). LBS was measured as the lifetime number of ringed (i.e. six day-old) chicks produced by each ringed chick.

This system has proved valuable for estimating additive genetic variances and covariances in key traits, including the degrees of female and male extra-pair reproduction (*77–81*), timing of breeding (*82*), occurrence of inbreeding (*83*) and measures of fitness (*67*). Recent analyses showed that there is substantial additive genetic variance in juvenile survival and adult male lifetime reproductive success, but very little additive genetic variance in adult female lifetime reproductive success (*67, 79, 81*). Such analyses are facilitated because the socially monogamous but genetically polygynandrous reproductive system generates numerous maternal and paternal half-sibs reared in the same and in different environments, and because dispersal within Mandarte means that there is no detectable spatial relatedness structure (*82*). Additive genetic variances and covariances are therefore likely to be adequately separated from environmental covariances. Please note however that previous analyses did not use the zero-inflated

Poisson models back-transformed to data-scale estimates presented here.

Collared flycatchers (*Ficedula albicollis*): Gotland, Sweden

Collared flycatchers (*Ficedula albicollis*) are small (∼13g), migratory passerines that winter in central Africa and breed in secondary tree cavities in parts of Europe and southwestern Asia. High site fidelity and limited natal dispersal (*84*) make them well-suited to studies of life-history variation, with an inter-annual survival rate for breeding adults of c. 45% (*85*). Male collared flycatchers will readily adopt nestboxes as potential breeding sites, which they defend from rivals and use to attract females. The female builds the nest and incubates the eggs, but both parents provision the chicks. Except for occasional replacement clutches, a single clutch of up to eight eggs is laid each year. Males are generally socially monogamous but – where the father is identified – a minority ($< 5\%$ (*86*)) are socially polygynous. However, additional females ($< 10\%$) may be mated to unrecognised polygynous males.

Our data were collected from nestboxes placed in the many scattered woodlots on the southern tip of Gotland (57°10′N, 18°20′E), an island in the Baltic Sea. Starting in early May, nestboxes are visited regularly to check for signs of nesting. Females are mainly caught while incubating clutches; males when provisioning chicks. Any previously unknown birds are fitted with a uniquely-numbered aluminium leg-ring, as are chicks. Note that the pedigree is based on observations of social relationships, and approximately 15% of nestlings are sired by an extra-pair male. Based on measures of lifetime reproductive success, defined as the number of young recruited to the breeding population, (*85*) reported a heritability of 0.008 ± 0.128 (estimate ± se) for lifetime reproductive success for male breeders and -0.014 ± 0.158 for female breeders, based on father-son and mother-daughter regressions, respectively. These were based on data from the first five years of this study (i.e., 1980-1984). Subsequent update based on larger samples reported heritabilities of 0.024 ± 0.079 and 0.041 ± 0.098 (*87*) and 0.07 ± 0.06 and 0.21 ± 0.06 (*88*) for LRS in male and female breeders, respectively, again based on parent-offspring regressions. More recently, additive genetic variances of age-specific 'annual genetic fitness' (AGF; note that AGF scores are absolute, rather than relative to the population mean) were estimated using animal models (and relying on 24 years of data) to be 0.013 ± 0.008 for males and 0.018 ± 0.008 for females (*89*), giving heritabilities of 0.031 ± 0.012 and 0.044 ± 0.013, respectively. Here, AGF was defined as the sum of a breeder's own survival to future breeding seasons (1 or 0) plus half the number of its offspring that recruit.

Hihi (*Notiomystis cincta*): Tiritiri Matangi and Tiritiri Matangi, Aotearoa New Zealand

Hihi (stitchbird, *Notiomystis cincta*) are an endemic passerine bird from the North Island of Aotearoa New Zealand. Hihi are sexually dimorphic in size (adult body mass – Male = 36 g, Female = 30 g) and plumage colouration. They are forest dwelling birds that feed on nectar, fruits and invertebrates (*90*). Hihi nest in cavities, breeding in the Austral spring between September and February from their first year of age and producing up to three clutches of 2-5 eggs per season, but usually only rearing two clutches successfully in a given year. The species is highly

promiscuous, with up to 70% extra-pair paternity (*91*), and the only bird species known to mate face-to-face (*92*).

The hihi are currently threatened as their range shrank to one remnant offshore population on the island of Hauturu-o-Toi (3083 Ha; 36°11′56.73″S, 175°4′53.15″E) in the late 1800s, due to habitat loss, introduced mammalian predation and the spread of disease by introduced avifauna (*93*). A reintroduction program was initiated in the 1980s, successfully re-establishing populations at seven new sites (*94*). Two of these reintroduced populations have been intensely monitored from founding to the present day: the population on the island of Tiritiri Matangi (220 Ha; 36.60°S 174.89°E) in the Hauraki Gulf since 1995, and the population on the mainland fenced reserve of Zelandia, Karori, Wellington (225 Ha; 41°17′39.75″S, 174°45′0.09″E), since 2005 (*94, 95*). Monitoring involves checking all nests at both sites daily from nest building to fledging. Chicks are bled or feather sampled for genetic analyses, morphology measured and ringed at 21 days of age. Every individual has a unique colour ring combination and metal identifier band. These are closed populations and there is no immigration or emigration. Pedigree reconstruction was achieved using monitoring data outlined above and genotyping every individual at 18 microsatellite loci (for details on sampling, DNA extraction and genotyping see - (*96*); for details on pedigree construction see - (*95, 97*)). This work is carried out under a New Zealand Department of Conservation permit held by John Ewen (36186-FAU, 15073-RES, 24128-FAU, 13939-RES and 44300-FAU). See hihiconservation.com, a website dedicated to the species' conservation efforts for further details.

LBS was estimated for each individual as the number of fledged individuals it produced in the pedigree. Previous work has detailed information on heritability, genetic variance and selection on a number of morphological, life-history and behavioural traits (*95, 97–99*). In particular, (*99*) estimated additive genetic variance in fitness to be very small using zero-inflated Poisson animal models. However, the estimate for additive genetic variance in fitness was reported from the Poisson and zero-inflation part separately and the total variance combining the zero-inflation and the Poisson processes was not computed.

Superb fairy-wrens (*Malurus cyaneus*): Canberra, Australia

Superb fairy-wrens are small songbirds (mass ca. 9g) which are widely distributed in south-eastern Australia (including Tasmania and offshore islands). They favour Eucalyptus woodland, but adapt well to suburban gardens and farmlands, provided that low cover is available to build nests. The birds mostly feed on very small arthropods, but feed their young larger prey. There is modest sex dimorphism (males are approximately 5% heavier), but extremely strong sex dichromatism, with males adopting a breeding plumage comprised of erectile pale and spectacular blue patches on the cheek, crown and nape. These patches are framed with a soft jet-black plumage. Females are dull brown. Predation on adults is modest, and probably mainly by accipiters and butcherbirds, though the latter are rare. By contrast, there is very heavy nest predation, particularly when pied currawongs are rearing their own young, as they mainly feed their nestlings young of other bird species. Other known nest predators include introduced and native mammals (red fox, black rat, brushtail possum), eastern brown snakes, and some birds (laughing

kookaburra and grey shrike-thrush).

The population of superb fairy-wrens in the native plantations of the Australian National Botanic Gardens has been colour-ringed and reproduction has been monitored since the breeding season that commenced in 1988 (from September to March 1989). Although the initial monitoring involved about 40 territories, the study area was more than doubled over 18 months in 1991/1992, reaching a peak density of 90 territories. The population is completely unclosed, being surrounded by contiguous unmonitored territories in all directions. The study aims to monitor every breeding attempt by a female during her life. DNA for parentage is collected from nestlings about 7 days of age. Paternity analysis is vital because most young are sired by males from outside the social group that provisions them (*100, 101*). Females produce 2-4 eggs, and can successfully produce 3 broods per season. Lifetime fitness data are complete for the individuals born in 25 cohorts from 1988 to 2012, subject to two caveats. First, some of the nestlings are sired by males from outside the study area, and conversely, some of the males gain success outside. Second, while males exhibit the greatest level of natal philopatry known (*102*), females disperse to take up a breeding vacancy (*103*), so some female young are lost, but they are replaced by immigrants.

The work is done under the auspices of the Australian National Botanic Gardens and the Australian Bird and Bat Banding Scheme, both of which are administered by the Dept of Environment and Energy of the Australian Government, and the Australian National University's Animal Experimentation Ethics Committee, which operates under guidelines established by the National Health and Medical Research Council. DNA for genetic analysis is obtained from blood samples collected by brachial venipuncture.

Although the study spans the advent of multilocus fingerprinting and used microsatellites for more than two decades, the pedigree used in this study was determined by analysis of paternity with a set of > 1360 autosomal SNPs. An exclusion method was applied that distinguishes the true sire from his close relatives, and to determine if the true sire has not been sampled (*104*). Particular attention in other studies of this population has been paid to the timing of nuptial moult in males, which predicts his success as an extra-group sire, and is under strong sexual selection ((*105, 106*).

Yellow baboons (*Papio cynocephalus*): Amboseli, Kenya

Baboons (genus *Papio*) are among the most well-studied of the cercopithecine primates (the old-world monkey sub-family that includes baboons, macaques and guenons). They are large, diurnal, omnivorous, semi-terrestrial monkeys with highly flexible and selective foraging abilities. They are primarily plant-eaters but readily consume invertebrates and small vertebrates. As a result of their ecological flexibility, baboons occupy a very wide range of environments, from near desert to temperate montane grasslands to moist evergreen forest. In doing so, they have achieved a nearly continental distribution in Africa (*107–109*). In addition, most baboon populations live in highly seasonal habitats, but typically show little or no seasonality in reproduction (*110, 111*). In other words, baboons have both adapted to diverse habitats and have broken free of the seasonal constraints of these habitats in major

aspects of their life histories, an ability shared by relatively few other primates.

Six species of the genus Papio are recognized, but genomic analysis indicates a complex history of admixture among these species, including ongoing hybridization at zones of contact ((*112*), see also (*113–115*)). The Amboseli baboons primarily exhibit yellow baboon phenotypes and ancestry (*Papio cynocephalus*), but they also experience natural admixture with neighboring populations of olive baboons (*P. anubis*). The most recent wave of such genetic admixture in Amboseli, during the past four decades, appears to have been preceded by repeated episodes of admixture during the evolutionary history of this population (*116–118*). The social systems of yellow and olive baboons are identical: populations are subdivided into stable social groups consisting of multiple adults and juveniles of both sexes. Males are approximately twice the size of females. Females remain in their natal group throughout life, while males typically disperse to other social groups, first in the late sub-adult or early adult period and then several more times throughout life. Females mate with multiple males, typically in the context of mate-guarding episodes that occur when females are in the ovulatory phase of their sexual cycle. Female baboons produce a single offspring with each birth; offspring are born relatively helpless, and depend upon mother's milk for nutrition until approximately 70 weeks of age (*119*).

The Amboseli Baboon Research Project monitors multiple social groups of baboons ('study groups') in the Amboseli ecosystem, located in southern Kenya (2° 41′ 10″S, 37° 12′ 30″ E). The research described here takes place with the permission of the Kenya National Council on Science, Technology, and Innovation (NACOSTI), under an agreement with the Kenya Wildlife Service (KWS), in a partnership that includes Duke University (USA), University of Notre Dame (USA), Princeton University (USA), the Institute of Primate Research (Kenya), and the University of Nairobi (Kenya). The research is conducted in compliance with all relevant research and animal welfare regulations in Kenya and the US. The Amboseli baboon population has been under continuous study since 1971; one study group was observed between 1971–1980, and a second study group was added in 1980. Permanent group fissions have happened several times, with the result that the number of study groups has varied over time (*120*). All animals in the study groups are individually known on sight based on morphological features. All demographic and life-history events (births, maturation events, immigrations, deaths and emigrations) are recorded on a routine basis as part of the near-daily monitoring of the study groups (*121*). For individuals born into the study population, birthdates are generally known to within a few days. For males that immigrate into the study population from the surrounding area, birthdates are estimated based on body size and physical characteristics (*122*). Females reach menarche at a median age of 4.5 years, and first birth at a median age of 6 years; males reach testicular enlargement at a median age of 5.4 years and achieve first mate-guarding at a median age of 7.5 years (*123*). Mortality in the first year of life has averaged 23% over the course of the study, and pre-adult mortality has averaged 44% for females and 50% for males (*124*). The Amboseli baboons have several natural predators in the ecosystem, including lions, spotted hyenas, snakes, and occasionally leopards.

For pedigree construction, maternities were identified from long-term records of births, and maternities and

paternities were verified with genetic parentage analysis. Microsatellite genotypes were obtained from DNA derived from fecal samples or, in some cases, blood samples. For samples extracted from feces, all apparent homozygous genotypes were reamplified at least four and up to seven additional times to guard against allelic dropout. All genotype data were produced on either an ABI 3700 Sequence Analyzer or an ABI 3730xl Sequence Analyzer. Parentage was assigned using the Cervus software, most recently version 3.0 (*125, 126*). Parentage analysis has been routinely conducted for the study population for over two decades, resulting in a pedigree with more than 1500 individuals (e.g., (*127–130*)).

LBS was measured as the number of offspring produced by each individual in the pedigree. Because male baboons disperse, the life history data for most males are incomplete. For males that are born in our study population but disperse away from it as subadults or young adults, we capture only the pre-adult phase. For males that immigrate into our study population, we capture part or all of the adult phase. A few males disperse from one study group to another, so that they spend part of all of their adult lives in the study population, and for these males our data are relatively complete. However, paternity assignments are never complete because many infants die before can obtain fecal samples for paternity analysis; thus information about number of offspring produced by each male is virtually always an underestimate. Our female life history data are complete for the cohorts included in our analyses. Female baboon fertility is affected by female dominance rank, which shows strong familial influences: daughters (but not sons) strongly resemble their mothers in the dominance rank they attain as adults, largely as a consequence of familial intervention in agonistic interactions (*131*). Male dominance rank is not subject to familial influence.

Rhesus macaques (*Macaca mulatta*): Cayo Santiago, Puerto Rico

Rhesus macaques are mid-sized primates (mean adult body length of 47cm for females, 53cm for males). They have the second widest geographic range of all primates (after humans), ranging from China to the Indian subcontinent. They are group-living, with groups containing multiple adult males and females, and mating is polygynous (*132*). Breeding is highly seasonal, with females only receptive to mating during half the year. Sexual dimorphism is low to moderate, and high-status males are unable to monopolise the majority of mating opportunities (*133*). Females produce at most one offspring per year (although twins occur on rare occasions). Juvenile mortality is low (10% for this population, for survival to one year), but for individuals that survive their first year of life, mean longevity is roughly 15 years for males and 20 years for females.

The Cayo Santiago population is a free-ranging colony located off the coast of Puerto Rico (18.1564° N, 65.7338° W). Established in 1938 with the introduction of 409 Indian-origin rhesus macaques, it is one of the longest monitored populations of animals in the world (*134*). The major causes of death for this provisioned and predator-free population are illness, old-age and injury, and there is no regular medical intervention for sick or wounded individuals (*135, 136*). Work takes place under the management of the Caribbean Primate Research Center and is regulated by the Animal Care and Use Committee of the University (IACUC) of Puerto Rico. The present study

took place under IACUC protocol number A6850108.

Demographic data have been collected up to 5 days a week since 1956. For all individuals, dates of birth and death are known to within a few days. Population control, involving the removal of mostly juveniles, is undertaken once yearly. All yearlings are marked under anesthesia with unique identifying tattoos on their chest and inner left thigh, and are given ear punches. DNA is collected from whole blood samples during this procedure. Parentage assignment is based on 29 microsatellite markers, with parentage known for most animals born since 1990 (ca. 2,886 monkeys) (*137, 138*). There is little evidence for loss of genetic diversity on Cayo Santiago, with little difference in blood polymorphism or mitochondrial haplotype diversity between this population and wild Indian rhesus macaques (*139, 140*). LBS was measured as the number of offspring attributed to an individual in the pedigree for every known individual. Monitoring data are available upon request from the Caribbean Primate Research Center: http://cprc.rcm.upr.edu/.

Previous work has documented the presence of heritable genetic variation and fitness correlates of numerous, especially social and morphological, traits (*137, 139, 141–146*), including some preliminary links to functional genetic variation (*137, 142, 147–149*). Ten years ago, additive genetic variation of female life history traits was found to be significant for lifespan, age at first reproduction, and LBS (*139*). Those estimates relied on Gaussian models and on a dataset that was half the size of the present study, and males were not examined.

Female rhesus macaques are philopatric, while males usually leave natal groups at puberty. Male dominance rank is established by queuing and physical combat, and is transient. Females form stable linear dominance hierarchies, with females securing ranks immediately below their mothers. The female hierarchy is further structured into matrilines, made up of closely related females that are close in rank (*132, 150*). Dominance rank is a partial predictor of fitness in this population (*136, 150*).

Snow voles (*Chionomys nivalis*): Churwalden, Graubünden, Switzerland

Snow voles are medium-sized rodents (adult body size 10-14cm plus 5-7.5cm for the tail). They are sparsely distributed in the rocky environments of southern Europe and Asia Minor, from sea level up to the highest mountain summits. Snow voles excavate burrows under the rocks or use natural clefts between rocks, sometimes carrying small stones to build walls (*151*). They are mostly, or perhaps strictly, herbivorous. In the Swiss Alps, snow voles' predators include red foxes, stoats, various owls and corvids, and their parasites include fleas, lice and ticks (*152*). The mating system is promiscuous and different individuals within the same litter can be sired by multiple males. Females normally produce 1 to 4 litters of 1 to 5 pups between May and September (*152*). Individuals generally do not reproduce in their first calendar year and may live up to a 3 years.

The snow vole study population is located in the Swiss Alps, near Churwalden (46°48' N, 9°34' E). It has been monitored from 2006 and we used records collected until 2017. The monitoring was authorised by the Amt für Lebensmittelsicherheit und Tiergesundheit, Chur, Switzerland. The study site is around 2,030 m above sea

level and consists of a 5ha scree surrounded by a steep cliff, meadows and forest. Given that snow voles are rock-dwellers, this configuration means that the population is spatially well defined and relatively isolated. The entire study area was trapped an average of 4 times per year, during the snow-free period from May to October. Pups are born between late June and late August, and most juveniles are captured at least once before winter. Upon capture, unknown individuals were tagged with a subcutaneous passive transponder (PIT, ISO transponder, Tierchip Dasmann, Tecklenburg) and an ear clip (maximum 2 mm in diameter) was taken using a thumb type punch (Harvard Apparatus) to later extract DNA. The population pedigree was reconstructed with the R package MasterBayes (*76*), one generation at the time based on 18 autosomal microsatellites developed for the population (*153*), on Y-linked marker and two mitochondrial markers (see details in (*154*)). LBS was measured as the number of offspring attributed to an individual in the pedigree for every known individual. Previous work has documented the presence of heritable phenotypic variation, natural selection and contemporary evolution of body mass in this population (*154, 155*). Additive genetic variance in relative fitness was previously estimated to 0.10 (95%CI $[0.06; 0.19]$) using a Gaussian animal model fitted to lifetime breeding success (*154*).

North American red squirrels (*Tamiasciurus hudsonicus*): Yukon, Canada

North American red squirrels (*Tamiasciurus hudsonicus*) are small tree squirrels distributed across boreal North America and south through the Appalachian, and Rocky Mountains (Steele, 1998). In the northern Boreal forest, red squirrels feed primarily on the seeds of white spruce (*Picea glauca*) (*156*). White spruce is a masting species that synchronously produces large number of seeds every 4-6 years with very low cone production during the intervening non-mast years (*157*). Red squirrels in this region cache spruce cones in a central larder hoard, and cached cones can last for several years, but this episodic seed production still has important effects on the population dynamics of red squirrels (*158*).

Red squirrels have been studied in the southwest Yukon Territory of Canada (61° N 138° W) continuously since 1989. The study area is within the traditional territory of the Champagne and Aishihik First Nations and the long-term research was performed through Scientists and Explorers Permits and Wildlife Research Permits in the Yukon Territory and with approval of institutional animal care committees. Since 1989, all individuals within 2-6 sub-populations have been individually marked and regularly monitored through live trapping and behavioural observations. Red squirrels are trappable, territorial, diurnal and conspicuous so individuals can be targeted for capture on their territory, and the death of an individual can be identified through its absence on its territory. Mortality prior to recruitment is high (*159*), but adults typically live to three or four years of age following recruitment (*159*). Maximum longevity in this area is eight years (*159*). In most years, females produce only a single successful litter of three or four offspring in spring (*159*). In mast years, however, females can produce two successful litters and litter sizes are larger (*160*). Natal dispersal distances are small (mean distance = 100 – 110 m; (*161, 162*)) relative to the size of the study areas (≈40 ha), and adults typically do not move territories ((*163*);

but see (*161*)). That said, there are undoubtedly some juveniles that successfully disperse outside the monitored populations (*164*) that are misassigned as being dead. Populations in the area experience predation from a natural community of predators (*165*).

Here we considered cohorts born between 1989 and 2009. All individuals within these cohorts were dead at the time of the analysis. Soon after offspring were born (6.8 ± 0.2 days; median = 5 days; mode = 2 days; (*159*), the location of their natal nest was located by radio-collaring their mother. At this time, offspring were temporarily removed from their natal nest and tissue was collected to determine paternity. Approximately three weeks later, offspring were temporarily removed from their natal nest again. At this age they were old enough to be permanently marked. Maternity was, therefore, known for all offspring born within the study area. Paternity, however, cannot be assessed behaviourally. Females mate with an average of seven males on their day of oestrus (*166*), males and females defend individual territories, and males provide no parental care. To assess paternity, tissue samples from newborn offspring have been collected since 2003 and were analyzed for cohorts between 2003 and 2014. DNA extracted from these samples was genotyped at 16 microsatellite markers to assign paternity (*166*).

In previous analyses, lifetime breeding success was found to have very low levels of direct genetic variance (*167*) and no evidence of differences in genetic variance in lifetime breeding success between the sexes or between environments (i.e., Genetic-by-environment interactions; (*167*)). There are, however, important maternal effects on lifetime breeding success and maternal genetic effects on lifetime breeding success, which provide some levels of indirect adaptive potential in this population (*168*).

Bighorn sheep *(Ovis canadensis)*: Ram Mountain, Alberta, Canada

Bighorn sheep are medium-sized artiodactyls (adult mass in the study population at Ram Mountain in September is 65-80 kg for females, 90-130 kg for males) distributed in mountain ranges in western North America from southern Canada to northern Mexico. They are predominantly grazers and rely on rugged escape terrain to avoid predators. At Ram Mountain, predation by specialist cougars (*Puma concolor*) can lead to population declines (*169*). Other predators include wolves (*Canis lupus*) and coyotes (*Canis latrans*). The mating system is polygynous. Males have large curled horns and dominant rams aged 7 years and older serially defend estrous ewes and obtain high mating success (*170*). In hunted populations (including the Ram Mountain study population), however, many rams with rapidly-growing horns are shot before they reach dominant status, leading to an evolutionary decline in horn size (*171*). Ewes can start reproducing at 2 years, but most ewes are primiparous at 3 years (*172*). Lamb survival is highly variable, but survival of prime-aged ewes (2–7 years of age) is usually above 90% (*173*). Maximum recorded longevity is 19 years for females and 14 years for males. In females, reproductive senescence starts at 13 years of age (*174*).

Ram Mountain is an isolated outcrop in central Alberta (52° N, 115° W) with about 38 km^2 of bighorn sheep habitat. The population has been monitored since 1971 (*175*) but paternity data are available only since 1987 (*170*).

A website is dedicated to presenting the monitoring: http://mouflons.pvp.ca/Ram%20Mountain.htm

For fitness data, we retained individuals marked after 1974, when the monitoring started being exhaustive. We discarded individuals born after 2006, because the reproductive success of these cohorts is still incomplete. Mother-lamb relationships are determined from suckling behavior, while paternity is assigned at 95% confidence based on about 30 microsatellites (exact number increased over time) and the program CERVUS (*176*). In some years, unknown rams arrive for the rut from other populations: sibships sired by these rams are identified using COLONY (*177*) but the identity of these fathers is unknown (*178*).

Over 98% of the population has been marked since 1975 with visual collars and ear tags. Fieldwork is conducted under the authority of a Province of Alberta Research permit (#19-072 for 2019) and a Université de Sherbrooke Animal Care Certificate (MFB-2018-01) to Marco Festa-Bianchet. Fieldwork lasts from late May to late September and involves recaptures in a corral trap baited with salt, in addition to field observations (*175*). lifetime breeding success was measured as the number of offspring known in the pedigree for each individual. An earlier analysis based on data collected up to 2003, and assuming a Gaussian distribution, found no support for heritability of lifetime recruitment success (number of offspring surviving to age one) for either sex (*178*).

Soay sheep (*Ovis aries*): St Kilda, NW Scotland

The Soay sheep is a small Bronze Age breed of domestic sheep. The study population has been living in a feral state without appreciable management in the islands of the St Kilda archipelago, Scotland, for an unknown period, possibly a few thousand years (*179*). Soay sheep are sexually dimorphic and polygynous: in the breeding season males defend oestrous females against other males; unsuccessful defence results in females mating with multiple males and sperm competition (*180*). Females may first become pregnant in their first year, at seven months, but more often do so in their second year of life (at about 19 months of age); most females have a single lamb each year but some have twins. The study population has no predators beyond great skuas taking a few neonates, but it has a range of gastrointestinal helminth and protozoan parasites and an ectoparasite, the sheep ked (*181*). The population experiences highly-variable winter mortality due to food limitation, weather and parasites (*182–184*) with entire lamb cohorts dying in some years. The Soay sheep population living in Village Bay on the island of Hirta, St Kilda (57°49′ N, 8°34′ W) has been monitored intensively since 1985 and we used records from this monitoring up to 2018 in this analysis. The works takes place under a UK Home Office Project Licence under the Animals (Scientific Procedures) Act 1986 as amended, current licence no PP4825594 held by J.M. Pemberton. The project takes place with the permission of the National Trust for Scotland, a charity which owns St Kilda. The population density of sheep is higher in Village Bay than the rest of the island due to the superior grazing, but the study population is continuous with that on the rest of the island and there is some immigration and emigration, particularly of males in the mating season. All lambs are tagged shortly after birth and monitored for the rest of their lives. DNA was obtained from ear punches removed during the tagging process. The population pedigree was reconstructed from

single nucleotide polymorphisms (SNPs; (*185*)) using the R package SEQUOIA (*186*) with some links from field observation or an earlier microsatellite-based pedigree included (*187*). More extensive description of the study is available at: http://soaysheep.biology.ed.ac.uk/.

There has been extensive previous quantitative genetic analysis of phenotypic trait variation in the population, particularly of traits measured at lamb capture or in the annual summer catch, parasite egg counts from faecal samples, and antibody levels from blood samples (e.g., (*185, 188–190*)).

Red deer (*Cervus elaphus*): Isle of Rum, NW Scotland

Red deer are large artiodactyls (adult body length of 160-210 cm for females, 175-250 cm for males). They are widely distributed in southwestern Asia, North Africa and Europe, and recently introduced in other parts of the world. The species is highly sexually-dimorphic and polygynous. Males develop antlers and defend harems of females during the breeding season (*191*). Females produce at most one calf per year. Juvenile mortality is high (for this dataset, survival to two years = 46%), but for individuals who survive to two years, average longevity is 8.7 years for males and 10.3 years for females. Red deer are strictly herbivorous. They have various parasites (*192*), and neonates may suffer predation by golden eagles.

The red deer study population is located in the North Block of the Isle of Rum, Scotland (57°01′ N, 6°17′ W). It has been intensively monitored from 1972; in this analysis, we used records collected until 2017 to compute fitness metrics. The work takes place under a UK Home Office Project Licence under the Animals (Scientific Procedures) Act 1986 as amended, current licence no 70/8818 held by J.M. Pemberton. The project takes place with the permission of NatureScot (formerly Scottish Natural Heritage), which manages the Isle of Rum National Nature Reserve. Within the ca. 12 km^2 of the study area, the population is un-managed and there has been no culling since 1973, although study individuals are occasionally shot when they visit surrounding areas. All calves are marked with ear tags (and a collar for females) shortly after birth, in order to record detailed life-histories of individuals throughout their lives (*191*). DNA was obtained from ear punches, post-mortem tissue and cast antlers. The population pedigree was reconstructed from single nucleotide polymorphisms as in (*193*), using the R package SEQUOIA (*186*); where DNA samples were not available, mother-offspring relationships are known from field observations. More extensive description of the study is available at: http://rumdeer.biology.ed.ac.uk/.

Previous work on the red deer has documented the presence of heritable genetic variation, genetic constraints and natural selection in numerous traits (e.g., (*194–199*)), and the evolution of phenology (*5*). In a previous analysis two decades ago, additive genetic variation in fitness was found not to be statistically significant and estimated at 0 in females and 0.1 in males (*200*). Those estimates relied on a smaller dataset, less exact pedigree reconstruction and less advanced statistical methods than the ones used in the present study.

Meerkats (*Suricata suricatta*): Kalahari, South Africa

Kalahari meerkats (*Suricata suricatta*) are sexually monomorphic social mongooses (adult body length approximately 30cm excluding tail, weighing between 0.5 and 1Kg) from southern Africa (*201*). They live in stable groups of 2-50 individuals, typically comprising one dominant female (either a founding member or born into the group) that is responsible for the majority of breeding attempts, a dominant immigrant male that fathers most of the young born to the dominant female, and a variable number of subordinate natal helpers. Meerkats cannot breed successfully without the assistance of helpers, and exhibit a range of cooperative behaviours including babysitting, allolactation, pup feeding, and sentinel duty. Only the dominant female breeds regularly, and can produce up to 4 litters of 1-7 pups annually. Breeding can occur throughout the year (although it commonly ceases in midwinter, April-July), and gestation length is approximately 70 days. Group size and dominance status have strong effects on the survival of pups (*202*). Infanticide by other pregnant females (either dominant or subordinate) is common, and subordinate females are all ultimately forced out of their natal group unless they acquire dominance. Meerkats are generally subject to high rates of mortality because they forage in open environments where visibility is high and they are exposed to predators (*203*). Meerkat groups defend their ranges (2-10km^2) against neighbouring groups, and these interactions can be lethal (*204*). In addition, meerkats are susceptible to social transmission of a novel strain of tuberculosis (*Mycobacterium suricattae*; (*205*)). Individuals can live for up to 13 years, although the reproductive performance of females begins to decline after they are five years old.

The Kalahari Meerkat Project (http://kalahari-meerkats.com/kmp/) has monitored a population of free-living meerkats at the Kuruman River Reserve in the southern part of the Kalahari Desert (26°58′S 21°49′E) continuously since 1993, involving detailed studies of more than 60 groups (with an average of 15 groups being monitored at any one time). All individuals in studied groups are dye-marked for field identification, tagged using unique subcutaneous transponder chips, and habituated to observation from within 1-2 metres. Dominant individuals are also fitted with radio collars to enable tracking of groups. Groups are visited up to twice per day on 3-4 days per week in order to record behaviour, weight, group composition and important life history events (e.g., pregnancy, birth, death, emigration and immigration). Upon first emergence from the natal burrow (approximately 3 weeks post-parturition), a 2-5mm tissue biopsy is taken from the tail-tip of each pup for genetic analysis. For recently habituated or immigrant adults, tissue samples are taken from anaesthetised or dead animals. Sampled individuals have been genotyped at up to 18 variable microsatellite loci, with genetic data available for over 65% of the total recorded population to date. The pedigree for the study population was reconstructed using a combination of microsatellite data, phenotypic descriptors and the parentage inference R package MasterBayes (*76*). Further details of pedigree reconstruction are provided by (*206*). Previous work in this population has shown high levels of inbreeding and evidence of inbreeding depression in a range of traits (*206*). Size parameters (mass at nutritional independence and asymptotic mass) are moderately heritable, but there is no evidence of a genetic basis for growth rates (*207*).

Spotted hyenas (*Crocuta crocuta*): Ngorongoro Crater, Tanzania

Spotted hyenas are large carnivores (adult body length is 125 cm for females and 121 cm for males in the Ngorongoro Crater). They are widely distributed in sub-Saharan Africa and inhabit a wide range of habitats. They live in social groups called 'clans' of up to 130 members (*208*). Clan social structure is characterised by a stable linear dominance hierarchy. The hierarchy is the result of disparities in social support between the clan members (*208*). Offspring of both sexes acquire a social rank just below that of their mother through behavioural support and social learning ('maternal rank inheritance') (*209*). The social rank in the hierarchy strongly determines fitness; high-ranking individuals survive better and produce more offspring than lower ranking individuals (*210, 211*). Furthermore, offspring of high-ranking mothers benefit from silver spoon effects; they grow faster, have a higher chance of survival to adulthood, start to reproduce earlier and have a higher lifetime reproductive success (*210, 212*). Dispersal is strongly male-biased, with approximately 85% of males and 1.5% of females leaving their birth clan and immigrating into another clan or founding a new clan in a vacated area (*211, 213*). The mating system is polygynandrous. All females reproduce, giving birth to 1 or 2 cubs (very rarely 3) per litter. Approximately 16% of twin and triplet litters are sired by more than one father. There is no distinct breeding season (*214*). Female investment in cubs is high: cubs are nursed for an average of 13 months with highly nutritious milk. Allonursing and adoptions are rare (*209*). Spotted hyenas live in 'fission–fusion' societies in which clan members often spend time alone or in small subgroups (*215, 216*). They hunt a large variety of prey species, ranging from springhares to buffaloes. In the Ngorongoro Crater, their preferred prey are wildebeest, gazelle fawns and buffalo calves (*217*). They usually hunt alone or in small subgroups. Lions are their main competitor for food and a major mortality factor. Another important mortality factor are pathogens; during the study period, a major outbreak of a disease caused by infection with a *Streptococcus bacterium* caused a 78% increase in mortality and annual population decline of 4.3% during two years (*218*). Juvenile mortality of individuals who were first observed at a young age ($<$ 1 month old) is 48% for females (n = 219) and 49% for males (n = 208). Mean lifespan of individuals who survived to the age at adulthood of 2 years and who were monitored for at least 15 years is 8.9 years for females (n = 154) and 8.2 years for males (n = 174).

The Ngorongoro Hyena Project (https://hyena-project.com/) has been monitoring all spotted hyenas of the eight resident clans inhabiting the 250-km^2 floor of the Ngorongoro Crater (3°11′ S, 35°34′ E) in Tanzania since April 1996. The population is genetically linked to neighbouring hyena populations outside the Ngorongoro Crater through male dispersal (*213*). Here, we used records collected until 2017. We retained individuals born until 2006 but used the later years to count reproductive success of those old cohorts. All hyenas are individually known by their spot pattern and other cues (*212*). Demographic and life-history data are collected routinely during near-daily visits of the study groups. Observations are made from a vehicle to which all hyenas are well habituated. DNA is isolated from tissue, faeces, skin biopsies, and hair. Tissue samples are collected opportunistically from dead animals. The epithelial layer of faeces is scraped off immediately after defaecation using a pocket knife. Skin

biopsies are collected using a Telinject GUT 50 dart gun fitted with a biopsy needle designed for spotted hyenas. Hair is plucked from cubs walking close to the vehicle using pliers. The population pedigree is reconstructed based on observed nursing, amplification of nine polymorphic microsatellites developed for spotted hyenas, and genetic parentage analyses using CERVUS 3.0 (*219*). Details about the parentage analyses can be found in (*211*). The full pedigree currently consists of over 2700 individuals. Lifetime breeding success was measured as the number of offspring produced by each individual in the pedigree. Because very few females leave their birth clan and most females and males who disperse join other study clans (*213*) we can monitor the life histories and calculate lifetime breeding success for most individuals of both sexes of our study population. Data and sample collection was approved by the scientific advisory board of the Tanzania Wildlife Research Institute, the Tanzania Commission for Science and Technology, the Ngorongoro Conservation Area Authority and the Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research. All study procedures were performed in compliance with the ethical regulations of these institutions.

Formulations of Fisher's fundamental theorem of natural selection

Fisher's fundamental theorem of natural selection has several formulations. Those formulations can be first classified based on whether they rely on 'Malthusian fitness' (fitness measured as a difference between a mortality rate and a birth rate), generally in continuous time, or 'Wrightian fitness' (fitness measured as the expected number of descendants produced in the next generation), generally in discrete time (*220*). Formulations based on Malthusian fitness can be found for instance in (*8, 9*), whereas formulations based on Wrightian fitness can be found for instance in (*12, 27, 221, 222*). The monitoring of wild vertebrate populations is typically discontinuous, which imposes the use of a discrete time, and our measure of individual fitness, lifetime breeding success, is Wrightian fitness. Therefore we used a formulation of Fisher's fundamental theorem based on Wrightian fitness.

Furthermore, the formulations of Fisher's fundamental theorem of natural selection can be classified based on the unit they express change in. We chose to use a formulation that expresses change in units of relative fitness, or equivalently in units of proportional increase in absolute fitness, as in (*27*) equation 6.17c, (*12, 14*). We can write this formulation as $\frac{\Delta\bar{W}}{\bar{W}} = V_A(w)$, where W is absolute fitness, $\bar{W}$ is mean absolute fitness, w is relative fitness, $V_A(w)$ is additive genetic variance in relative fitness. This formulation can also be written $\Delta\bar{w} = V_A(w)$.

A common alternative formulation of the theorem expresses change in units of absolute fitness, as the additive genetic variance in absolute fitness divided by mean absolute fitness: $\Delta\bar{W} = V_A(W)/\bar{W}$ (where $V_A(W)$ is additive genetic variance in absolute fitness), as in for instance (*9, 222, 223*), (*27*) equation 6.20b. Those two formulations are mathematically equivalent, as shown in (*27, 221*), as they express the same result in different units, and differ only by a factor $1/\bar{W}$.

Here, we choose to use $\frac{\Delta\bar{W}}{\bar{W}} = V_A(w)$ rather than $\Delta\bar{W} = V_A(W)/\bar{W}$ for several reasons. First, $V_A(w)$ is a mean-standardized metric, and an evolvability (*19*), and hence can be compared across different systems. In a sense, our study is a meta-analysis so it was essential to convert estimates from different studies to a common scale. Expressing effects relative to the mean is one of the most common and useful scales (*19*), especially natural for a strictly positive quantity such as fitness. In addition, the estimation of mean and variance parameters for absolute fitness is necessarily noisy because with field data there is always measurement error in the measure of individual absolute fitness, in particular due to differences in protocol. For instance, differences in the rate of emigration in each population, necessarily introduces artefactual variation in $\bar{W}$ and $V_A(W)/\bar{W}$, but have no impact on $V_A(w)$. Such differences could be merely a function of an arbitrary decision to monitor a certain area in each population, rather than reflecting any biological differences. On a technical note, generalised linear mixed models using Poisson distributions tend to generate both large variances and means, in the sense that the posterior predictive distribution usually generates many more outliers than the actual data contains, and so expressing the results based on variance in absolute fitness would introduce artefactual variation. However, the bias in variances is proportionate to the bias in squared means, so taking a variance / mean^2 (as in $V_A(w) = V_A(W)/(\bar{W}^2)$) avoids this artefact.

Finally, $\frac{\Delta\bar{W}}{\bar{W}} = V_A(w)$ is the formulation used in both reviews of the fundamental theorem of natural selection

in wild populations (*12, 14*). These reviews set the baseline against which we compare our results quantitatively, and we needed to use the same metric to be able to compare our results to theirs.

For completeness we provide estimates of $V_A(W)/\bar{W}$ in supplementary text S6.

Statistical methods

Earlier models of fitness that did not assume a Gaussian distribution

Most previous studies have estimated $V_A(w)$ with models that assume a Gaussian distribution for residuals, but a few studies have used transformed measures of fitness (*200*) or Poisson distributions (*67, 167*): these better capture right-skew but still do not allow for zero-inflation. Further, parameters from log-transformed or Poisson models are estimated on a transformed (link) scale and not on the scale of the original raw data, which is the scale required to measure rates of adaptation as $V_A(w)$. Finally, a few studies of plants in experimental settings have used the 'Aster' method which can fit lifetime fitness well if individual fitness components are measured finely enough to be modeled with conventional generalised linear models (*224*).

The zero-inflated Poisson animal model

For each population we fitted an animal model of individual absolute lifetime breeding success using a zero-inflated Poisson model. We then subsequently back-transformed link-scale estimates of additive genetic variance and covariances, integrating over fixed and other random effects, to obtain data-scale estimates of additive genetic variance in relative fitness. This approach is an application of the more general methods described in (*33*); see also (*15, 34, 35*).

In zero-inflated Poisson models, the response variable (here absolute fitness measure, W, of an individual i) is modelled as the product of a Bernouilli process $\mathcal{B}$ with probability p_i and a Poisson process $\mathcal{P}$ with expectation λ_i:

$$W_i = \mathcal{B}(1 - p_i)\mathcal{P}(\lambda_i). \tag{1}$$

The Bernouilli process's probability p_i corresponds to the excess probability of having a zero fitness value, over and above that expected from the Poisson process, and is modelled as a linear predictor (l_1) on a logit-link scale:

$$p_i = \text{logit}^{-1}(l_{1,i}) \tag{2}$$

$$= 1/(1 + \exp(-l_{1,i})), \tag{3}$$

(note the convention that higher values of $l_{1,i}$ correspond to lower values of $1 - p_i$, and hence higher probability of a zero value).

Conditional on $\mathcal{B}(1 - p_i) = 1$ (i.e., that an individual is not part of the excess zeroes), an individual's fitness value follows a Poisson distribution $\mathcal{P}(\lambda_i)$, where $\lambda_i = \exp(l_{2,i})$ and $l_{2,i}$ is a second linear predictor. Zero-inflated

models therefore have two linear predictors, $\boldsymbol{l_1}$ and $\boldsymbol{l_2}$.

We describe in detail a model with a basic combination of fixed and random effects that was common to all models, but also fitted some additional effects specific to particular populations (for instance, social group in social species). We also tried different combinations of fixed and random effects to ensure that results were robust to the choice of fixed and random effects (see supplementary text S4); please see Table S3 for further details on other variables fitted in the respective models. For the two linear predictors, l_1 and l_2:

$$l_{1,i} = \boldsymbol{X_1 b_1} + a_{1,i} + m_{1,i} + c_{1,i} + e_{1,i} \tag{4}$$

$$l_{2,i} = \boldsymbol{X_2 b_2} + a_{2,i} + m_{2,i} + c_{2,i} + e_{2,i}, \tag{5}$$

where $\boldsymbol{X_1}$ and $\boldsymbol{X_2}$ are design matrices and $\boldsymbol{b_1}$ and $\boldsymbol{b_2}$ are fixed effects of (for both $\boldsymbol{l_1}$ and $\boldsymbol{l_2}$) pedigree inbreeding coefficient (computed with the R-package Pedantics (*225*)), cohort (as a continuous variable), sex and "genetic group" (*36*), in order to account for structure in the base population (see below for details about fixed effects).

The a, m and c in equations (4) and (5) are random effects associated with additive genetic values, maternal effects, and cohort effects respectively, and the e are error terms.

The fixed effects are estimated independently in the two linear functions, but the random effects follow Gaussian joint-distributions with covariation between the zero-inflated and the conditional-Poisson components. In particular, the additive genetic values for the two components, $\boldsymbol{a_1}$ and $\boldsymbol{a_2}$, follow:

$$\begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} \sim \mathcal{N}\left(\mathbf{0}, \begin{bmatrix} \sigma^2_{a1}\mathbf{A} & \sigma_{a12}\mathbf{A} \\ \sigma_{a12}\mathbf{A} & \sigma^2_{a2}\mathbf{A} \end{bmatrix} \right), \tag{6}$$

where $\boldsymbol{A}$ is the additive genetic relatedness matrix derived from the pedigree, σ^2_{a1} is the additive genetic variance for the zero-inflation component, σ^2_{a2} the additive genetic variance for the conditional-Poisson component, and σ_{a12} is their additive genetic covariance. The maternal values follow:

$$\begin{bmatrix} \boldsymbol{m_1} \\ \boldsymbol{m_2} \end{bmatrix} \sim \mathcal{N}\left(\mathbf{0}, \begin{bmatrix} \sigma^2_{m1}\mathbf{I} & \sigma_{m12}\mathbf{I} \\ \sigma_{m12}\mathbf{I} & \sigma^2_{m2}\mathbf{I} \end{bmatrix} \right), \tag{7}$$

where $\boldsymbol{I}$ is the identity matrix, and the σ^2_m are maternal-level variances in the two processes and their covariance. Note that we are not attempting to separate maternal genetic and environmental components, but simply modelling variation between offspring of different mothers, over and above that due to the additive genetic effects.

The cohort values follow the same structure as the maternal values:

$$\begin{bmatrix} \boldsymbol{c_1} \\ \boldsymbol{c_2} \end{bmatrix} \sim \mathcal{N}\left(\mathbf{0}, \begin{bmatrix} \sigma^2_{c1}\mathbf{I} & \sigma_{c12}\mathbf{I} \\ \sigma_{c12}\mathbf{I} & \sigma^2_{c2}\mathbf{I} \end{bmatrix}\right) . \tag{8}$$

The errors follow:

$$\begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix} \sim \mathcal{N}\left(\mathbf{0}, \begin{bmatrix} 1\mathbf{I} & 0 \\ 0 & \sigma^2_{e2}\mathbf{I} \end{bmatrix}\right) , \tag{9}$$

where $\boldsymbol{I}$ is the identity matrix, and σ^2_{e2} the over-dispersion variance in the conditional-Poisson process, that can be thought of as the amount of unexplained among-individual variance in the Poisson process. The over-dispersion variance in the Bernouilli zero-inflation process is not identifiable and has to be fixed to an arbitrary value (here we used 1). The covariance between the errors in the two processes is undefined because the Poisson process is conditional on the zero-inflation and therefore the error covariance is fixed to zero.

Bayesian implementation

All models were fitted in R version 3.6.3 using the Bayesian package MCMCglmm version 2.29 (*38*). For the fixed effects, we used Gaussian priors with means of zero and a variance of 10 (the default variance of 10^{10} gave slow and poor MCMC mixing in the zero-inflation part of the model for some populations). For the random effects, we used parameter expanded priors with degree-of-belief parameter (nu) equal to 3, working mean equal to 0, and working variance equal to 1,000. We ran models for a minimum of 130,000 iterations (with a burnin of 30,000 and a thinning interval of 100), but generally for 10 times longer or as long as necessary to obtain posterior effective sample sizes of at least 200 for all parameters (in most models at least 600). Each model was fitted independently three times to check consistent convergence. For each model, convergence was assessed by visual examination of the three MCMC chains traces and posterior density distributions (checking for lack of trends, presence of a single mode, efficient mixing, and overlap of the three chains) and by checking that Gelman-Rubin's $\hat{R} < 1.1$ (*226*) (for $V_A(w)$ the largest $\hat{R}$ of any model was 1.046).

Back-transformation of parameters to the data scale

For each random effect, we then transformed the link-scale estimates of the variance-covariance matrix for the two link linear predictors (the zero-inflated component and the conditional-Poisson component) of the absolute fitness, to a single estimate of variance in relative fitness on the data scale using the methods presented in (*33, 34*).

The data-scale variances associated with each random effect can be obtained as the variance in data-scale expected absolute fitness values, marginal on the focal random effect and integrated over other random effects and fixed effects. To obtain variances in relative (rather than absolute) fitness, those variances are then divided by

squared mean expected absolute fitness (*34*). To obtain the additive genetic variance on the data-scale the method is slightly different, because breeding values on the data scale are the part of the phenotype that depends linearly on the link breeding values ((*227*), see also (*35*)), and applying the previous method to the additive genetic random effect returns a data-scale genetic variance that sums additive and non-additive components (*34, 35*). Therefore, as shown in (*33, 34*), the additive genetic variance in relative fitness on the data-scale can be computed as $V_A(w) = \boldsymbol{d^T G d}$, where $\boldsymbol{G}$ is the link-scale additive genetic variance-covariance matrix, and $\boldsymbol{d} = (d_1, d_2)$ is the vector of average partial derivatives of mean relative fitness with respect to the link linear predictors l_1 and l_2. Those derivatives were obtained by calculating finite differences in mean fitness following perturbations in mean latent values, and Monte-Carlo integration over all random effects and fixed effects on each linear predictor. The calculations were then also integrated over the full posterior distributions.

Once all variance components had been obtained on the data scale, we divided them by the phenotypic variance in data-scale relative fitness (that is, the 'opportunity for selection', (*228*)), to obtain the proportions of variance, including the narrow-sense heritability in fitness (*229*).

Alternative fixed and random effect structures

In the main text we present results from "full" models containing fixed and random effects chosen both based on general principles about the estimation of quantitative genetic parameters, and on the particularities of each population (for the structure of models in each population see table S3). Here we first explain the reasons for including each of the fixed and random effects that appear in the "full" models. We then give the structure of simpler models that we fitted for each population in order to assess the robustness of the estimation of $V_A(w)$ to model structure (Table S4).

We included an individual's pedigree inbreeding coefficient as a fixed covariate in all models to avoid a potential bias in estimates of additive genetic variance-covariance parameters (*230*). Pedigree inbreeding generally increases in more recent generations, as more of the ancestry of individuals is known in the pedigree, and is not an accurate measure of individual inbreeding. Therefore estimates for the effect of pedigree inbreeding should not be interpreted as accurate estimates of inbreeding depression.

We included cohort, as a fixed covariate, to correct for potential biases in the estimation of breeding values through time in the case of directional change in mean fitness driven by the environment (*37*). However, when including cohort as a fixed effect in the zero-inflation part of the model, the intercept and the parameter for cohort had trouble converging in the models for rhesus macaques and spotted hyenas, although the convergence issue did not affect the estimate of $V_A(w)$. Because neither the population-specific estimates nor the meta-estimates of $V_A(w)$ were sensitive to the inclusion of this effect, we decided to simplify the reporting of our analyses and fitted cohort as a fixed effect only in the conditional Poisson part of the model for all populations.

We included an indicator of genetic group, as a fixed covariate, the proportion of genome of immigrant origin,

estimated from the pedigree while assuming that individuals in the first cohort form a base population (*36*). Accounting for a genetic group captures some of the structure in the individuals with unknown parents to distinguish between local genetic changes and gene flow (for example, an individual with one immigrant parent would have a value of 0.5). We define immigrants as individuals with unknown parents, excluding individuals in the first earliest cohorts which constitute the base population. These individuals may be true immigrants from other distant populations, individuals originating from outside the margin of continuous populations, or rarely local individuals whose parents were never sampled. Accounting for different genetic backgrounds reduces the possible bias that gene flow can introduce in the estimates of the amount of additive genetic variation existing within the local population. However, the parameter estimates for genetic groups should not be interpreted as the true effect of gene flow because some individuals considered immigrants in the calculation of genetic groups are not true immigrants. The effect of genetic group varied substantially between the different populations (Table S7), but the inclusion of the effect had little influence on the estimation of $V_A(w)$; see results in supplementary text S4).

We included sex, as a fixed factor, to account for potential differences in estimates of mean lifetime breeding success among sexes in our datasets. Biologically females and males should have the same mean lifetime breeding success. Nevertheless, small differences in sampling between the sexes may generate differences in mean lifetime breeding success among sexes in each dataset, as may situations where female reproductive success is more reliably known (e.g. from field observations) than male (which may require genotyping that is not always available for all individuals). Accounting for sex likely improves the fit of models. In 5 of the bird populations, sex was unknown in a substantial proportion of individuals that died or disappeared early (Table S1), and therefore had a lifetime breeding success of zero. Rather than discarding those records we used random sex assignments for individual with unknown sex. For comparison, we also re-ran models without including sex as a predictor, and did not observe changes in estimates of $V_A(w)$ (see SI supplementary text S4).

In populations of social species, if the pattern of social inheritance of social dominance rank is correlated with the pattern of genetic inheritance (e.g. if offspring dominance rank is determined socially by the dominance rank of their parents, (*208*)), one may expect additive genetic parameters to be biased upward. In the four social species where the existence of stable social rank inheritance is known (yellow baboons, rhesus macaques, meerkats, and spotted hyenas), we therefore included fixed effects for individual social rank, to reduce the potential for social inheritance to contaminate the estimation of additive genetic parameters. The exact specification differed among species based on prior knowledge of each species. In rhesus macaques, social rank was fitted as a three-level factor (high, medium or low rank). In meerkats, we fitted a two-level factor (dominant or not). In the yellow baboons and spotted hyenas, we fitted a continuous variable with values between 0 and 1 indicating the quantile of the rank of an individual at birth. For spotted hyenas, we also fitted ordinal rank, a continuous variable with non-null integer values, indicating the absolute rank of an individual at birth (where 1 is highest dominance rank, and large values indicate more subordinate individuals). We included an interaction between sex and social rank in baboons, and

fitted social rank only for females in rhesus macaques and spotted hyenas.

However, in all four social species, the mechanisms of social inheritance of dominance are quite complex, subtle and variable, so that dominance status is generally very variable among close kin. The confounding between genetic inheritance and social inheritance is therefore likely to be much weaker than one might expect at first. We explored these issues in depth with individual-based simulations of the spotted hyena population in the Ngorongoro Crater (see supplementary text S5); these analyses indicated that social rank inheritance does not substantially bias the estimation of additive genetic variance. Moreover, if social dominance is partly caused by traits that are genetically inherited, such as body size or aggressiveness, accounting for social status may in fact bias genetic parameters downwards. We chose to be conservative and include social status in the main models, although in the end, the estimates of $V_A(w)$ were almost insensitive to the inclusion of social status (supplementary text S4).

We also included a series of random effects: additive genetic effects in order to estimate $V_A(w)$, maternal identity ('mother') to account for maternal effects and other non-genetic sources of similarity between siblings, and cohort (as a factor) to account for temporal variation in environmental conditions, in particular the effect of early-life conditions on lifetime reproductive outcome (*231*). In addition, we included an interaction between maternal identity and cohort, to account for the additional similarity expected from siblings born in the same year. In the main text we report the sum of the variance among mothers and the variance corresponding to the mother-by-year interaction as 'maternal variance'. This interaction was fitted for all populations except for the red deer, which was the only species in which mothers never give birth to more than one offspring per year. In the meerkats we also included a random effect for litter, which is known to explain variation in life-history traits in this species (*202*). Finally, for the rhesus macaques, meerkats and spotted hyena populations, we also included a random effect for social group, as those populations are subdivided into groups or clans.

Table S3: Structure of the models presented in the main text for each population. Effects are fitted for both the zero-inflation and the conditional-Poisson parts of models, except for the fixed effect of cohort which was fitted only to the conditional-Poisson part. Bold text highlights variables that are not fitted for every population (see text).

Populations	Fixed effects	Random effects
btM, btP, btR, gtH, gtW, spM, cfG, hhT, hhK, sfC, svG, rsK, bsR, ssS	Inbreeding + Cohort (covariate) + Genetic group + Sex	Additive genetic + Mother + Cohort + **Mother:Cohort**
rdR	Inbreeding + Cohort (covariate) + Genetic group + Sex	Additive genetic + Mother + Cohort
ybA	Inbreeding + Cohort (covariate) + Genetic group + **Sex*Social rank**	Additive genetic + Mother + Cohort + **Mother:Cohort**
ybA	Inbreeding + Cohort (covariate) + Genetic group + **Sex*Social rank**	Additive genetic + Mother + Cohort + **Mother:Cohort + Social group**
rmC, shN	Inbreeding + Cohort (covariate) + Genetic group + Sex + **Social rank (in females)**	Additive genetic + Mother + Cohort + **Mother:Cohort + Social group**
mkK	Inbreeding + Cohort (covariate) + Genetic group + Sex + **Social rank**	Additive genetic + Mother + Cohort + **Mother:Cohort + Social group + Litter**

Note: btM= blue tit at Muro, btP= blue tit at Pirio, btR = blue tits at la Rouvière, gtH=great tits at Hoge Veluwe, gtW = great tits at Wytham Woods, spM= song sparrows on Mandarte, cfG= collared flycatchers on Gotland, hhT=hihi on Tiritiri Matangi, hhK= hihi at Karori, sfC= superb fairy-wrens in Canberra, ybA = yellow baboons at Amboseli, rmC= rhesus macaques at Cayo Santiago, svG=snow voles in Graubünden, rsK=red squirrels in Kluane, bsR=bighorn sheep on Ram mountain, ssS=Soay sheep on St Kilda, rdR=red deer on the Isle of Rum, mkK=meerkats in the Kalahari, shN= spotted hyenas in the Ngorongoro Crater.

Table S4: Effects successively removed from the main model. Alternatives 1 and 2 remove effects for a subset of populations whereas 3 and 4 remove effects from all populations. Effects removed in alternative n are also absent in alternatives $> n$.

Model	Populations	Effects changed
Alternative 1	ybA, rmC, mkK, shN	*minus* Social rank
Alternative 2	All (except rdR)	... *minus* Mother:Cohort
Alternative 3	All	... *minus*+ Genetic Group
Alternative 4	All	... *minus* Sex

Note: ybA = yellow baboon at Amboseli, rmC= rhesus macaque at Cayo Santiago, mkK=meerkat in the Kalahari, shN= spotted hyena in the Ngorongoro Crater, rdR=red deer on the Isle of Rum.

Meta-analytic estimates

After obtaining posterior distributions for the variance parameters ($V_A(w)$, $V_M(w)$, $V_C(w)$) and the proportions of variance (h^2, m^2, c^2, expressed as percentages) in relative fitness on the scale of the data in each of the 19 populations, we computed meta-estimates of each variance parameter following a posterior sampling framework ((*232*) in which the framework is called 'multiple imputation' given the similarity to models used to deal with missing data) in the R-package brms (*233*). For each parameter, we generated 100 tables (each composed of one row for each population), drawing from the posterior samples of the focal parameter: either $V_A(w)$, $V_m(w)$, $V_c(w)$, h^2, m^2 or c^2. We fitted a linear mixed model of each of these parameters with population as a random effect. For the intercept we tried three different priors without any effect on the posterior distribution: a Gaussian distribution of mean 0 and standard deviation 20, a Gaussian distribution of mean 0 and standard deviation 20 folded to cover only positive values, and a uniform distribution over $[0; 20]$. For the random effect standard deviation and the residual standard deviation, the prior was a half-Cauchy distribution of parameters 0 and 1 (note that in brms the prior is set for standard deviations instead of for variances like in MCMCglmm). We used the global intercept from the model of each parameter as the meta-estimate average for that parameter, and report the standard deviation in the random effect of population as a measure of variation in parameter estimates among populations. We also report the posterior mode and 95% highest posterior density credible interval for each meta-estimate.

Calculation of the maximal rate of trait response to selection

The value of $V_A(w)$ in a population sets an upper bound to the per-generation response to selection of any trait. That upper bound can be expressed, in units of phenotypic standard deviations for a trait z, as $\sqrt{{h_z}^2 V_A(w)}$, where ${h_z}^2$ is the heritability of z. The inequality can be derived from Robertson's secondary theorem of natural selection in its form published in (*234*) and explained page 165 of (*27*), which states that the response to selection in z (R_z) is the covariance between the additive genetic values for relative fitness (A_w) and the additive genetic values for the trait (A_z):

$$R_z = \mathrm{cov}(A_w, A_z)$$

$$\text{by definition of a correlation, } R_z = \mathrm{cor}(A_w, A_z)\sqrt{V_A(w)V_A(z)}$$

$$\text{and because a correlation is always less than 1, } R_z \leq \sqrt{V_A(w)V_A(z)}.$$

Note that for simplicity and without loss of generality, we define z so that $\mathrm{cov}(A_w, A_z) \geq 0$. If the covariance is negative, one can simply consider the response in $z' = -z$ instead of z.

Therefore we have:

$$\frac{R_z}{\sqrt{V_A(z)}} \leq \sqrt{V_A(w)}.$$

$$\begin{aligned} \text{By definition, the heritability of } z \text{ is } {h_z}^2 &= \frac{V_A(z)}{V_P(z)} \\ \text{so, } \sqrt{V_A(z)} &= \sqrt{{h_z}^2 V_P(z)} \\ &= \sqrt{{h_z}^2}\mathrm{SD}_P(z) \end{aligned}$$

Therefore, we can express the upper bound of the per-generation response to selection in trait z, in units of phenotypic standard deviations of z, as $\frac{R_z}{\mathrm{SD}_P(z)} \leq \sqrt{{h_z}^2 V_A(w)}$

For example, for ${h_z}^2 = 0.30$ (an average value of heritability in wild populations, (*28*)) , and $V_A(w) = 0.185$ (our meta-analytic average), we get $\frac{R_z}{\mathrm{SD}_P(z)} \leq 0.236$.

Supplementary text

S1 Goodness of fit

Analysing lifetime fitness in wild populations is a thorny statistical challenge, and previous models that have been used in the past were potentially biased because of their intrinsic limitations. For instance linear mixed models (Gaussian models, fitted to relative fitness data) often predict some negative fitness values, can only accommodate a single mode for the distribution of values, and will generally over-estimate the frequency of low-intermediate values and underestimate the number of zeroes and of high values. Over-dispersed Poisson or negative-binomial generalized linear mixed models (fitted to absolute fitness data) can also accommodate only a single mode and generally cannot capture a high frequency of zeroes. This lack of fit can produce substantial biases in the estimation of variance parameters, including $V_A(w)$ (*15*).

In the 19 datasets analysed here, our zero-inflated over-dispersed Poisson always provided a better fit than the models mentioned above. To visualise the fit, we simulated lifetime breeding success values according to the zero-inflated Poisson model structure and parameter estimates for each population. For each population, for each posterior sample and for each individual in the dataset we drew a simulated lifetime breeding success value and summarised the distribution of individual lifetime breeding success values within each population. We plotted the posterior distribution of simulated lifetime breeding success distributions on top of the actual distribution of lifetime breeding success in each population (birds in Fig. S1, mammals in Fig. S2). In most populations we did not observe any substantial deviation between the observed and simulated distribution of lifetime breeding success. We plotted

95% distributions of the simulated values, so we may expect 5% of lifetime breeding success values to fall outwith the simulated intervals. However there were a few apparent deviations. In some populations, the models predicted some very rare non-zero values that were never observed in the actual data (e.g., 2 and 3 in Muro blue tits, btM, also some cases in other blue tits, snow voles, yellow baboons, bighorn sheep, see Fig. S1 and S2). In the collared flycatcher population, the fit was imperfect for small lifetime breeding success values Fig. S1, perhaps because the observed distribution has three modes whereas the model accommodates two modes. In the macaque population, the proportion of zero is under-predicted and the rest of the distribution is slightly over-predicted Fig. S2, presumably because the observed distribution of lifetime breeding success between 1 and 12 was almost uniform, which does not conform well to an over-dispersed Poisson distribution. Nevertheless, for the large majority of populations and range of values, the the zero-inflated Poisson distributions fitted the observed data well.

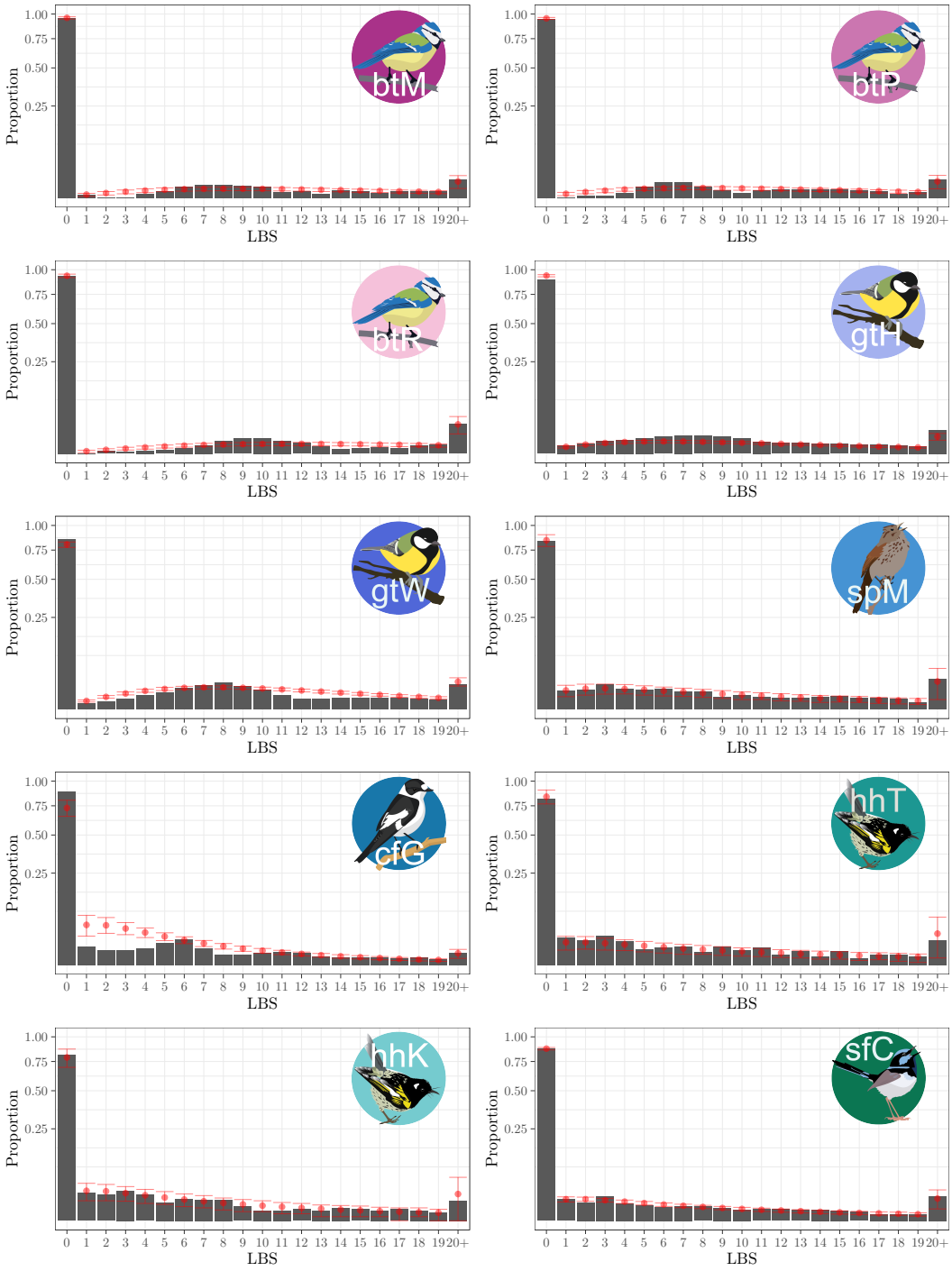

Figure S1: **Comparison of observed and predicted distributions for lifetime breeding success in bird populations**. Grey bars represent observed raw data. Red points and error bars represent mean and 95% credible intervals of model simulations. For ease of visualisation, the y-axis is on a square-root scale and lifetime breeding success values of 20 or more are grouped together in one category. btM=blue tits at Muro, btP=blue tits at Pirio, btR = blue tits at la Rouvière, gtH=great tits at Hoge Veluwe, gtW=great tits at Wytham Woods, spM= song sparrows on Mandarte, cfG=collared flycatchers on Gotland, hhT= hihi on Tiritiri Matangi, hhK= hihi at Karori, sfC= superb fairy-wrens in Canberra.

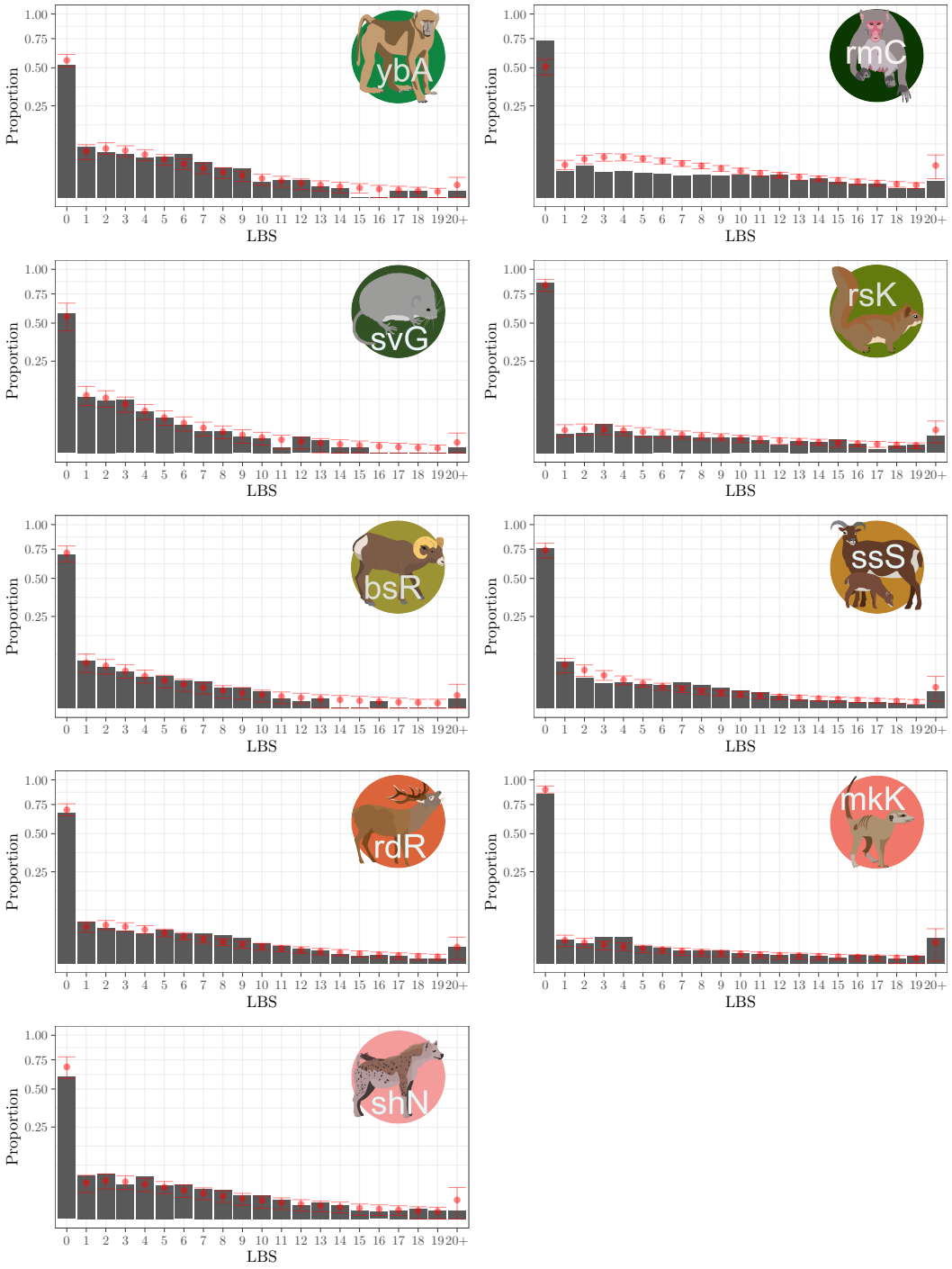

Figure S2: **Comparison of observed and predicted distributions for Lifetime Breeding Success in mammal populations**. Grey bars represent observed raw data. Red points and error bars represent mean and 95% credible intervals of model simulations. The y-axis is on a square-root scale. Lifetime breeding success values of 20 or more are grouped together in one category. ybA= yellow baboons at Amboseli, rmC=rhesus macaques at Cayo Santiago, svG=snow voles in Graubünden, rsK=red squirrels at Kluane, bsR=bighorn sheep on Ram Mountain, ssS= Soay sheep on St Kilda, rdR=red deer on the Isle of Rum, mkK=meerkats in the Kalahari, shN=spotted hyenas in the Ngorongoro Crater.

S2 Prior distribution of $V_A(w)$

We set explicit priors on the link scales for all fixed and random effect parameters. However, the prior distribution of $V_A(w)$ was not explicitly defined in our model because $V_A(w)$ is a transformed parameter, that does not appear in the model definition. However, it is important to know the prior distribution of $V_A(w)$ to check that the posterior distribution is primarily influenced by the data rather than by the prior.

We approximated the prior distribution of $V_A(w)$ by drawing random numbers from the prior distributions of all random and fixed effects and then applying the back-transformation method for $V_A(w)$ to each of these random draws. The range of $V_A(w)$ values in the prior is much greater than the range of values in empirical posterior distributions so we had to draw a larger number of prior samples (10^6 instead of 10^3) to obtain a smooth visualisation of the prior in the range of values of interest (approximately from 0 to 2).

The prior distribution of $V_A(w)$ was weakly informative for very small values of $V_A(w)$: The distribution had a mode of approximately 0.0014, was dense for values below the mode (3.3% of the probability mass) and covered large values (42% of the probability mass above 1, 5% above 10). The prior did not appear to influence the posterior distribution in any population (Fig. S3).

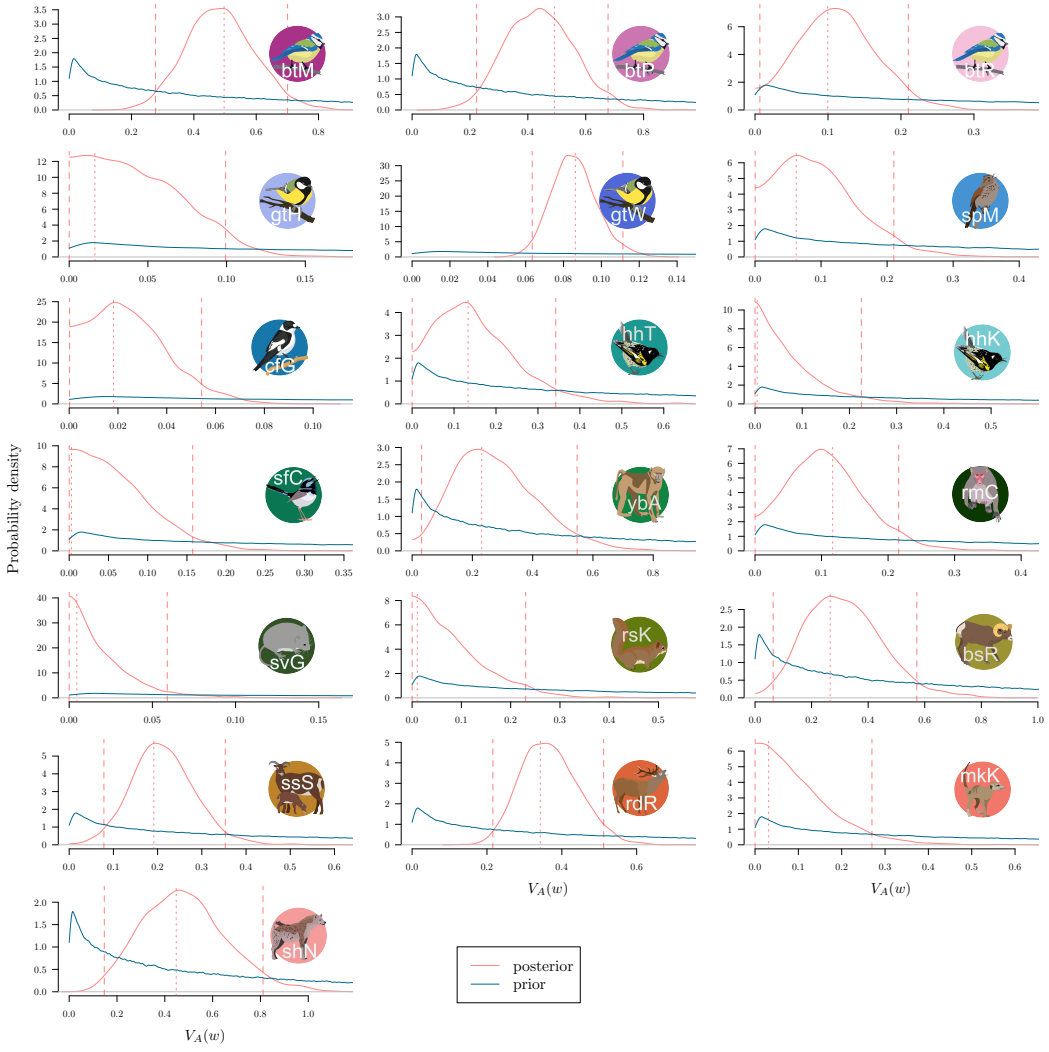

Figure S3: **Prior and posterior distributions of $V_A(w)$ in each population**. The vertical red lines show the posterior mode (dotted) and 95% credible interval (dashed). The area under each curve sums to one, but in the case of the priors only 68% of the area is visible at most as the distribution extends to far larger values. Posterior distributions correspond to the models presented in the main text. Note the different x- and y-scales for each population.

S3 Relative speed of adaptation

What qualifies as a "large" or a "small" value of $V_A(w)$ is in part arbitrary, but considering a specific time window relevant to our study, we propose some rough benchmarks that may help interpret and discuss our results. In a first thought experiment, we consider individual relative fitness w, estimated relative to mean fitness in the base generation. Assuming a stable environment and a constant $V_A(w)$, the mean fitness g generations later is expected to be $\bar{w_g} = (1 + V_A(w))^g$. We can conceptualize $\bar{w_g}$ as a comparison of the mean performance of individuals from generation 0 that were dormant and are then resurrected, to the performance of individuals in the generation g, when the two pools of individuals are made to compete in a common environment (a type of experiment that exists in micro-organisms, for instance (*235*)). Any non-null value of $V_A(w)$ leads to unrealistically large values of $\bar{w_g}$ after a sufficiently large number of generations, but within a given range of generation numbers, different values of $V_A(w)$ may correspond to biologically meaningful differences in $\bar{w_g}$. For our 19 populations, the mean number of pedigree generations (length of lineages in the data-sets) varies from 1.87 to 16.63 (table S2), with a mean of 4.4 and a median of 3.6. We therefore considered the expected dynamics of $\bar{w_g}$ for up to 5 generations.

For $V_A(w) = 0.01$, after 5 generations, mean fitness relative to the first generation mean fitness, reaches only 1.16, which may not be easily perceptible given the large demographic and environmental stochasticity typical of wild populations (*236*). However for $V_A(w) = 0.05$, mean fitness would have doubled after 5 generations (Fig. S4A), which is appreciable. For $V_A(w) = 0.3$, mean fitness would more than double after only 2 generations, and would be predicted to reach 51 after 5 generations. Such a rate of increase in mean fitness is absurdly large and would likely not manifest itself in nature beyond 1 or 2 generations, at which point density-dependent or frequency-dependent processes would likely erase the increase in fitness relative to a distant generation (*237*). In addition, $V_A(w)$ is unlikely to remain constant through time, both because the strength of selection is likely to decrease as the population adapts to the new conditions and because the response to selection may generate gametic-phase disequilibrium (*238*). Therefore we propose that in the context of studying adaptation over a handful of generations, values of $V_A(w) < 0.01$ can be considered 'small', values of $0.01 \leq V_A(w) < 0.05$ 'moderate', values of $V_A(w) \geq 0.05$ 'large' and values of $V_A(w) \geq 0.3$ 'very large'.

We can confirm the value of these benchmarks by considering another thought experiment, that we will refer to as an evolutionary rescue thought experiment: A population is perfectly adapted and at equilibrium in a given environment when a sudden and permanent environmental change reduces mean absolute fitness by some arbitrary but instructive amount, say, one third. Ignoring any potential effects of decreased population density, without any adaptive evolution the population size would decline by 1/3 every generation, and would eventually become so small that extinction by demographic stochasticity would be inevitable. To isolate the effect of adaptive evolution, we assume a constant value of $V_A(w)$ and a constant environment, in particular we ignore factors such as overlapping generations, demographic stochasticity and density dependence. Under those conditions, if $V_A(w) > 0$ and if the adaptive potential represented by $V_A(w)$ is realised as per-generation increases in mean absolute fitness, evolution

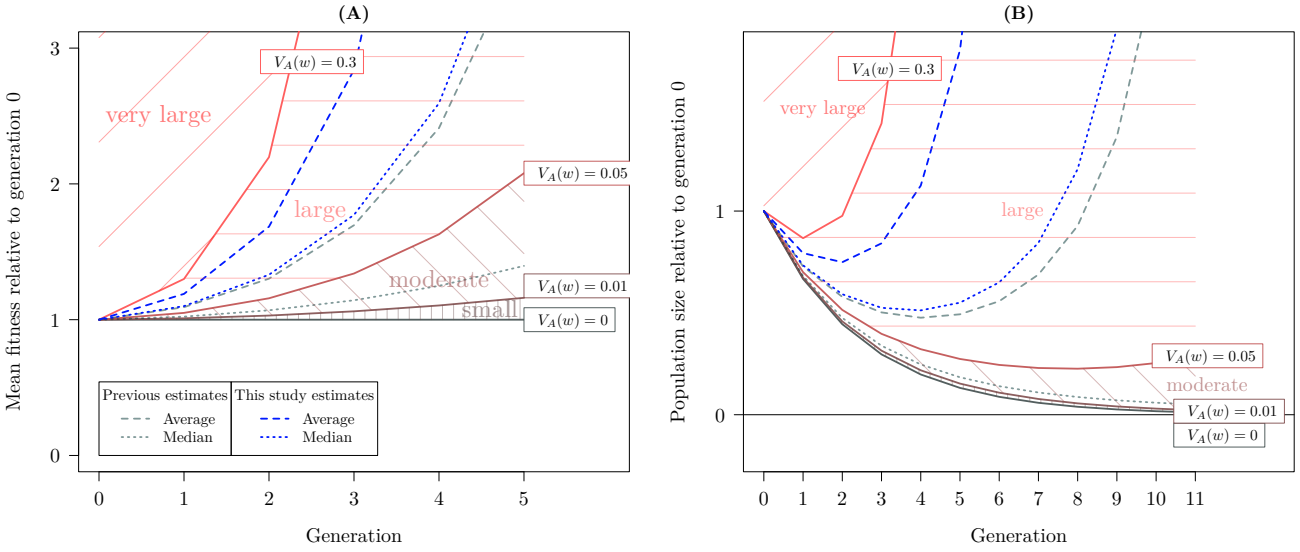

Figure S4: **Illustration of what constitutes a large value of $V_A(w)$ over 5 to 10 generations shown by:** (**A**) Considering the dynamic of fitness relative to generation 0 as a function of additive genetic variance in relative fitness ($V_A(w)$); (**B**) Considering population size across 11 generations relative to generation 0 after a sudden and permanent environmental change that reduces mean fitness by 1/3. Values of $V_A(w)$ between 0 and 0.01 are considered small. In both panels we assume a constant $V_A(w)$, constant environment, no density- or frequency-dependent selection. Empirical meta-estimates are shown in dashed/dotted lines: in grey, projections using the average and median of previously published estimates, in blue, projections using the average and median of estimates produced in this study.

may 'rescue' the population (*239*), the population eventually recovers when the predicted population size equals or exceeds the initial population size. Note that the value of $V_A(w)$ itself does not directly predict population dynamics, but only the proportional per-generation change in mean fitness. In turn, mean fitness does predict population dynamics. We can project the expected demographic trajectory by increasing the population growth rate (λ) by a factor of $(1 + V_A(w))$ each generation: for generation 0, $\lambda_0 = 2/3$; for generation $g > 0$, $\lambda_g = \lambda_{g-1}(1 + V_A(w))$. The population size for each generation is given by $N_{g+1} = \lambda_g N_g$. The recovery is faster for larger values of $V_A(w)$ and takes place in about 3 generations for $V_A(w) = 0.3$, 16 generations for $V_A(w) = 0.05$, 81 generations for $V_A(w) = 0.01$ (Fig. S4B). The pedigrees included in this study have a maximal depth covering a number of generations ranging from 4 (in hyenas) to 38 (in great tits in Wytham Woods) with a median of 12 generations (note that we are here talking about maximal depth, whereas in the first paragraph of this section we mentioned average depth). Therefore, in the context of our study, it can be argued again that $V_A(w) < 0.01$ is 'small' as it does not allow recovery within the time-frame of any of our studies, values between 0.01 and 0.05 are 'moderate' as they may allow for partial, but not full, recovery during the time-frame of our studies, $V_A(w) > 0.05$ is 'large' as it allows a recovery within about 16 generations (close to the median number of pedigree generations), $V_A(w) > 0.3$ is 'very large' as it allows a recovery within about 3 generations (less than our shortest pedigree).

S4 Estimates of $V_A(w)$ in models with different fixed and random effect combinations

Figure S5 shows the estimates of $V_A(w)$ from models that differed in their random and fixed effect structures, and specifically in their inclusion or not of sex, genetic group, maternal-cohort interaction and social dominance rank. In most populations, different fixed and random effect combinations yielded similar estimates of $V_A(w)$. More complex models yielded sometimes higher, sometimes lower, posterior modes for $V_A(w)$. The average meta-estimate for $V_A(w)$, across all populations, was almost entirely insensitive to the different combinations (table S5).

Table S5: Meta-estimates for the average of $V_A(w)$ and its standard deviation among populations, for different sets of models.

	Average $V_A(w)$			Std. Deviation $V_A(w)$		
Model	Estimate	SE	95% CI	Estimate	SE	95% CI
Main models	0.19	0.06	[0.09 ; 0.30]	0.12	0.07	[0.01;0.26]
Alternative 1: ... *minus* SocialDom	0.18	0.06	[0.08 ; 0.30]	0.11	0.06	[0.01; 0.25]
Alternative 2: ... *minus* Mat:Cohort	0.20	0.06	[0.08 ; 0.32]	0.12	0.07	[0.01;0.27]
Alternative 3: ... *minus* GG	0.22	0.08	[0.09 ; 0.38]	0.15	0.09	[0.01; 0.34]
Alternative 4: ... *minus* Sex	0.21	0.07	[0.08 ; 0.35]	0.14	0.08	[0.01;0.31]

Notes: Estimates are posterior modes, SE are estimated standard errors, and 95%CI are computed with highest posterior density. All meta-estimates are computed from the 19 populations, sometimes with different model structures. The 'Main Models' meta-estimates were computed from models presented in the main text, which included the fixed effects of Social Dominance for ybA, rmC, mkK and shN. The 'Alternative 1' meta-estimates were calculated from models which were the same as the Main Models except for excluding Social Dominance (for these 4 populations). The 'Alternative 2' models were the same as 'Alternative 1', except for the exclusion of 'Maternal:Cohort' (for all populations except rdR, for which this random effect was never fitted). The 'Alternative 3' and 'Alternative 4' models then dropped Genetic Group and Sex in turn (see section S2.2.4 for more details).

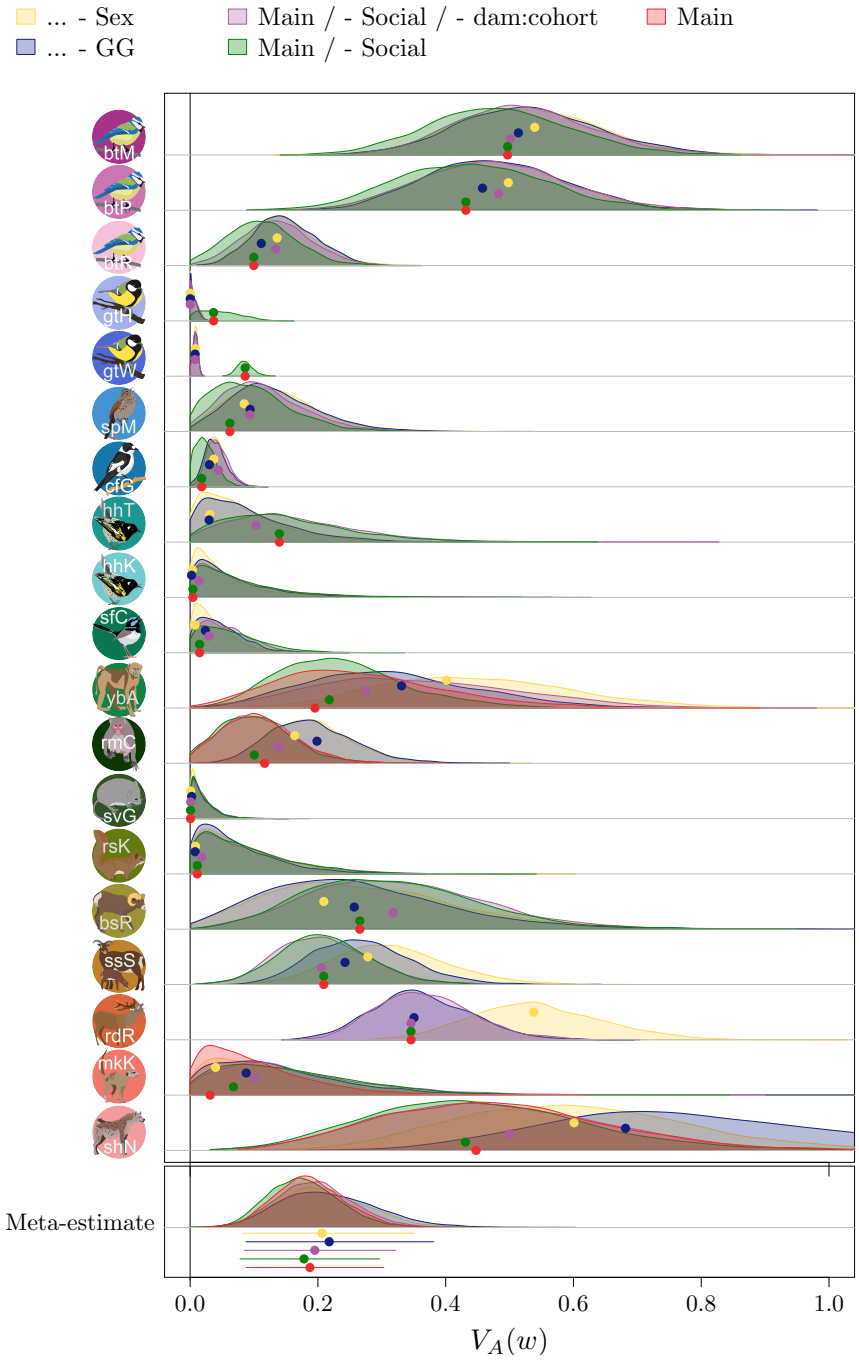

Figure S5: **Posterior distributions of $V_A(w)$ in each population and their meta-estimates for different combinations of fixed and random effects**. Filled curves show the full posterior distributions and dots show posterior modes (at an arbitrary y-coordinate). Some distributions are fully overlapping and not distinguishable. For meta-estimates of the average $V_A(w)$ (bottom row), the dots show the posterior mode and horizontal lines show 95% credible intervals. See model definitions in supplementary methods. All meta-estimates are computed from the 19 populations, sometimes with different model structures. The "Main" meta-estimate (in red) was computed from models presented in the main text, which include social rank for ybA, rmC, mkK and shN, and include dam:cohort for all populations except rdR. The "Main / − Social" meta-estimate (in green) was calculated from "alternative 1" models which include dam:cohort, except for rdR. The "Main / − Social / − dam:cohort" meta-estimate (in purple) was calculated from "alternative 2" models for all populations. The "... − GG" (in blue) was calculated from "alternative 3", and the "... − Sex" (in yellow) from "alternative 4" models for all populations.

S5 Social inheritance of social rank in spotted hyenas

We explored the effect of social inheritance of dominance rank on estimates of $V_A(w)$ using a case study of the spotted hyena population. To do this, we simulated individual-level data following a complex model of spotted hyena life-history including the inheritance of social rank and an influence of social rank on fitness components. All functions representing life-history processes were parameterized with the empirical data of the spotted hyena population used in the study, often using smooth functions from generalized additive models (GAM). The life-history functions allowed for density dependent relationships as a function of both population size and clan size. Both density-dependent terms interacted with individual rank. These simulations did not contain any genetic variance and potential similarity between relatives is purely the result of social inheritance.

We analysed each of the 100 simulated dataset with two series of zero-inflated over-dispersed Poisson animal models and back-transformed variance parameters as for empirical data. First, we used a model that does not include information of individual social rank to assess how much our estimations of $V_A(w)$ may be artifactually biased by social inheritance in such a system. Second, we re-fitted the model with a fixed effect for birth rank, standardized within cohort, to assess whether this effect reduced the potential bias in estimates of $V_A(w)$ and changed the estimation of other random effects.

In brief, we found no substantial bias in estimates of $V_A(w)$ when not accounting for social inheritance in the animal models (Fig. S6). The modal estimate value for $V_A(w)$ was very close to zero as expected under the absence of genetic variance and most of the variance due to social inheritance turned out to be absorbed by over-dispersion variance.

Simulation algorithm for analysis of social inheritance of social rank in spotted hyenas

We initialised simulations using the empirical founder population composition on 12/04/1996, and run for 25 years with a time step of 1 month. Each individual life-history was then summarised to compute lifetime breeding success, the population pedigree and other fixed and random effects necessary to fit the animal model. As with empirical studies, we retained focal individuals born until 2006, but used the later part of the simulation period to count reproductive success of focal individuals. The model was run in R using R6 for encapsulated object oriented programming.

For every time step (month), we determine in sequence:

1. whether each individual survives to the next time step
2. for surviving males, whether they disperse, allowing them to join a different clan
3. for surviving females, we determine reproduction (probability of reproduction, probability of having twins, and calculation of birth rank)
4. the rank of each individual is updated based on the introduction of new individuals

Many of the life-history functions use GAM smooth functions, with different functions being used for the top ranking individuals and for the lower ranking individuals. Each GAM smooth functions use a different smoothing parameter (λ) that within each function varies depending on the years of data used to fit the model.

The individual survival probability for females is computed as the logit of a linear function that includes an effect of current total population size, an effect of current clan population size, an effect of individual rank, the interactions between population sizes and individual ranks, and a clan-specific intercept.

$\text{logit}(p_{sf}) = s_{\lambda sf1}(a|\text{top}) + s_{\lambda sf2}(a|\text{lower}) + s_{\lambda sf3}(e) + \beta_{rsf}r + \beta_{clansf} + \beta_{Nsf}N + \beta_{nsf}n + \beta_{r:Nsf}rN + \beta_{r:nsf}rn$, where:

- p_{sf} is the survival probability
- $s_{\lambda sf1}(a|top)$ is the GAM smooth function of age for females in the top 5 ranks of their clan in month m.
- $s_{\lambda sf2}(a|lower)$: GAM smooth function of age for females outside the top 5 ranks of their clan in month m.
- $s_{\lambda sf3}(e)$: GAM smooth function of observer effort in the 12 months before and including month m. Field protocol in the Ngorongoro Crater classifies an individual as dead if they have not been observed for at least 12 months. The probability for an individual to be unobserved during a 12 month period, and therefore to be classified as dead, will be affected by observer effort in the clan during the previous year.
- β_{rsf} is the effect of rank on survival, and r is the rank of the focal female.
- β_{clansf} is a clan-specific intercept corresponding to where a female was located in month m.
- β_{Nsf} is the effect of total population size, summed over all clans, on female survival, and N is current total population size.
- β_{nsf} is the effect of clan population size on female survival, and n is current clan population size.
- $\beta_{r:Nsf}$ and $\beta_{r:nsf}$ are interactions between rank and populations sizes.

Pre-dispersal male survival has a probability computed as:

$\text{logit}(p_{smb}) = s_{\lambda smb1}(a|top) + s_{\lambda smb2}(a|lower) + \beta_{\text{clan, smb}} + \beta_{rsmb}r + s_{\lambda smb3}(e) + \beta_{psmb} + \beta_{Nsmb}N + \beta_{nsmb}n + \beta_{r:Nsmb}rN + \beta_{r:nsmb}rn$, where

- $s_{\lambda smb1}(a|top)$ is the GAM smooth function of age for males in the top 5 ranks of their clan in month m.
- $s_{\lambda smb2}(a|lower)$: GAM smooth function of age for males outside the top 5 ranks of their clan in month m.
- $\beta_{\text{clan, smb}}$ is a clan-specific intercept
- β_{rsmb} is the effect of rank on survival, and r is the rank of the focal male.

- $s_{\lambda smb3}(e)$ is the GAM smooth function of observer effort in the 12 months before and including month m.
- β_{psmb} is the effect the focal male being born to a primiparous mother
- β_{Nsmb} is the effect of total population size, summed over all clans, on male survival, and N is current total population size.
- β_{nsmb} is the effect of clan population size on male survival, and n is current clan population size.
- $\beta_{r:Nsmb}$ and $\beta_{r:nsmb}$ are interactions between rank and populations sizes.

Post-dispersal male survival has a probability computed as:

$\text{logit}(p_{smp}) = s_{\lambda smp1}(a) + \beta_{\text{clan, smp}} + \beta_{rsmp}r + s_{\lambda smp2}(e) + \beta_{Nsmp}N + \beta_{nsmp}n + \beta_{r:Nsmp}rN + \beta_{r:nsmp}rn$, where

- $s_{\lambda smp1}(a)$ is the GAM smooth function of age among males post-dispersal
- $\beta_{\text{clan, smp}}$ is a clan-specific intercept
- β_{rsmp} is the effect of rank on survival, and r is the rank of the focal male.
- $s_{\lambda smp2}(e)$ is the GAM smooth function of observer effort in the 12 months before and including month m.
- β_{Nsmp} is the effect of total population size, summed over all clans, on female survival, and N is current total population size.
- β_{nsmp} is the effect of clan population size on female survival, and n is current clan population size.
- $\beta_{r:Nsmp}$ and $\beta_{r:nsmp}$ are interactions between rank and populations sizes.

Models for post-dispersal males do not include any term for rank or primiparity as we expect these variables to no longer be important once males leave their natal clan: dispersing males go to the bottom of the hierarchy in new clans so there is very limited variation in the rank category of individuals (*211*).

Dispersal. All mature males ($\geq$ 24 months) have a chance to disperse from their current clan. Firstly, we consider whether or not a male prospects for new clans. Males that have not left their natal clan (including philopatric males) will always prospect. For a male that is outside its natal clan the chance to prospect is set to the empirical probability estimated from dispersal behaviour in the Ngorongoro Crater.

For those males that do prospect, the probability of dispersing to a given clan is determined from a multinomial distribution where probability of selecting a given clan is equal to the proportion of all young females (1 - 5yo) living in the crater that are found in the clan. This age range is based on work by (*213*) concerning spotted hyena dispersal.

Reproduction. All females $\geq$ 36 months old without dependent cubs are considered ready to reproduce. The probability for a female to successfully reproduce during any time step is simulated using a general additive model fitted with a binomial response with a logit link using data from the Ngorongoro Crater.

Potential males are determined by the female-mate choice rule (*213*). Assuming there is more than one potential male, the female will select the one with the highest tenure (i.e., that has inhabited the clan the longest). When no potential males are present in a time-step based on the mate choice rule females will forgo reproduction. Gestation always leads to at least one offspring. Probability of producing a twin litter is simulated using a general additive model fitted with a binomial response with a logit link using data from the Ngorongoro Crater.

The probability of successful reproduction, p_R, for a given female is: $\text{logit}(p_R) = s_{\lambda R1}(a|top) + s_{\lambda R2}(a|low) + s_{\lambda R3}(e) + \beta_{rR}r + \beta_{clanR} + \beta_{NR}N + \beta_{nR}n + \beta_{r:NR}rN + \beta_{r:nR}rn$

- $s_{\lambda R1}(a|top)$ is the GAM smooth function of age for females in the top 5 ranks of their clan in month m.
- $s_{\lambda R2}(a|lower)$: GAM smooth function of age for females outside the top 5 ranks of their clan in month m.
- $s_{\lambda R3}(e)$: GAM smooth function of observer effort in the 12 months before and including month m.
- β_{rR} is the effect of rank, and r is the rank of the focal female.
- β_{clanR} is a clan-specific intercept corresponding to where a female was located in month m.
- β_{NR} is the effect of total population size, summed over all clans, and N is current total population size.
- β_{nR} is the effect of clan population size, and n is current clan population size.
- $\beta_{r:NR}$ and $\beta_{r:nR}$ are interactions between rank and populations sizes.

Given successful reproduction, the probability of twinning (as opposed to having a single cub) given successful reproduction, p_t, is given by:

$\text{logit}(p_t) = s_{\lambda t1}(a|top) + s_{\lambda t2}(a|low) + s_{\lambda t3}(e) + \beta_{rt}r + \beta_{clant} + \beta_{Nt}N + \beta_{nt}n + \beta_{r:Nt}rN + \beta_{r:nt}rn$

- $s_{\lambda t1}(a|top)$ is the GAM smooth function of age for females in the top 5 ranks of their clan in month m.
- $s_{\lambda t2}(a|lower)$: GAM smooth function of age for females outside the top 5 ranks of their clan in month m.
- $s_{\lambda t3}(e)$: GAM smooth function of observer effort in the 12 months before and including month m.
- β_{rt} is the effect of rank, and r is the rank of the focal female.
- β_{clant} is a clan-specific intercept corresponding to where a female was located in month m.
- β_{Nt} is the effect of total population size, summed over all clans, and N is current total population size.
- β_{nt} is the effect of clan population size, and n is current clan population size.

- $\beta_{r:Nt}$ and $\beta_{r:nt}$ are interactions between rank and populations sizes.

Note that three-cub litters are rare in reality and are not considered in the simulation. Another simplification is that in the simulation, multi-cub litters always have the same father, whereas in the studied populations twin siblings are sometimes sired by different males. This simplification should tend to increase the bias in $V_A(w)$ in simulations compared to the empirical data.

Rank calculation. Ranks are defined within each clan. The dominant female has a rank of 1, higher ranks mean lower dominance status. The rank of a newborn is determined by the rank of the mother. If the mother is of rank r, the newborn will be born with rank $r+1$. All individuals with a rank previously $> r+1$ have their rank increased by 1.

Bias in estimates of $V_A(w)$ without correction for social inheritance of social rank in spotted hyenas

When not accounting for social inheritance in the model, we estimated $V_A(w)$ to 0.0241 on average, with a median of 0.0076 among the 100 datasets. The prior distribution for $V_A(w)$ had a mode close to 0.002, so social inheritance did appear to generate a small bias on the posterior distribution of $V_A(w)$. Some point estimates (14%) were moderately large ($V_A(w) > 0.05$), but the 95% confidence interval excluded small values ($V_A(w) > 0.01$) in only 1% of simulations (Fig. S6). The bias was therefore very small and could not explain the empirical estimate of 0.448, 95%CI $[0.147; 0.811]$, in this population. Apart from the additive genetic variance, other variance components were small except the over-dispersion (Fig. S6).

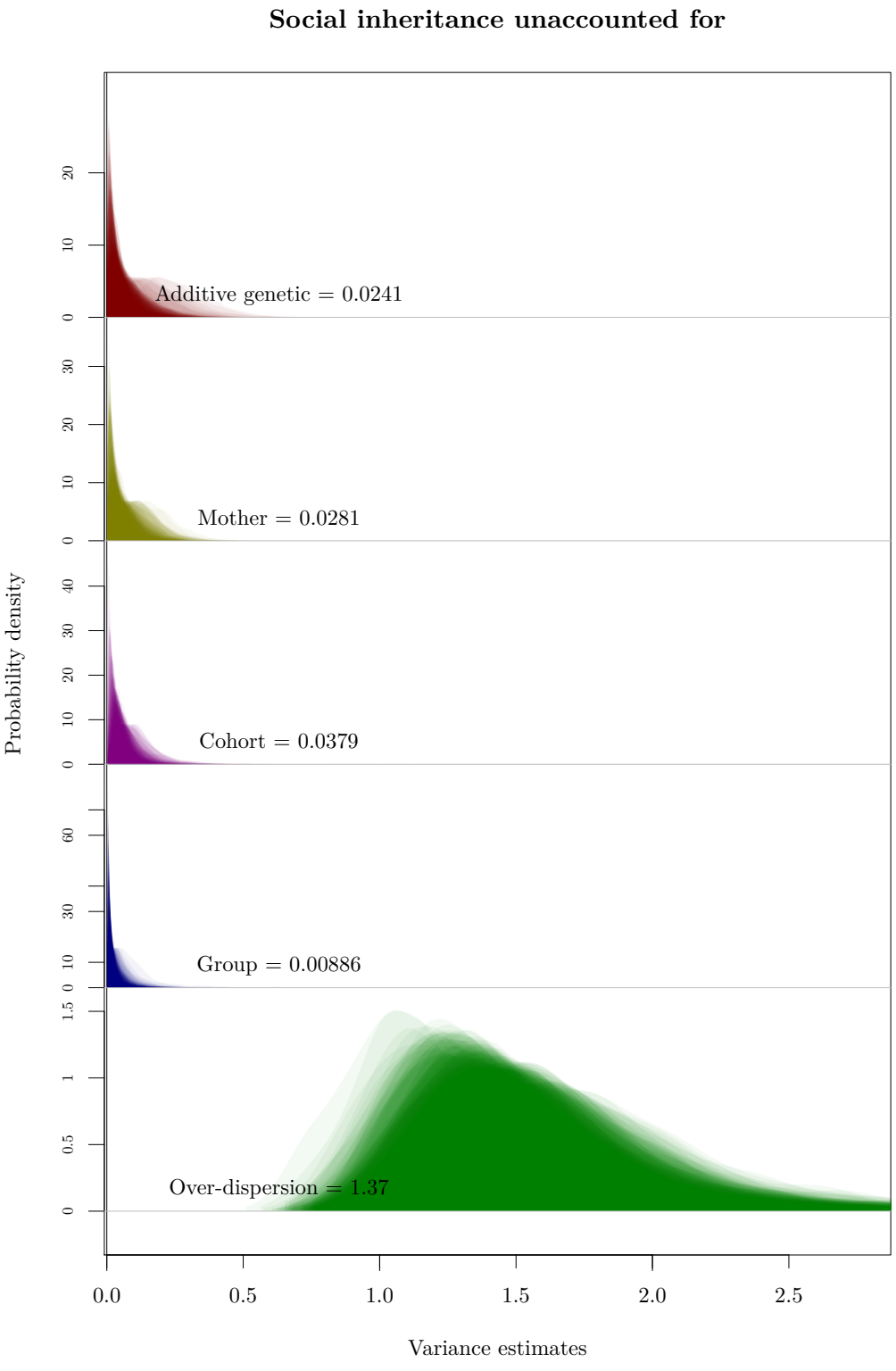

Figure S6: **Posterior distributions of variance components on the data-scale for the 100 simulated spotted hyena datasets when analysed without correction for social inheritance**. The number on each row are averages of point-estimates among the 100 datasets.

Bias in estimates of $V_A(w)$ with fixed effect correction

We re-fitted the model to the 100 datasets adding a fixed effect for individual birth rank, standardized within cohort. The estimates for the effects of birth rank was as expected, with a small increase in the probability of zero-inflation with increasing rank (estimate 0.09, SD 0.33) and a small decrease in the conditional-Poisson expectation (estimate 0.33, SD 0.08).

When accounting for social inheritance, compared to models without correction, the most striking difference was the decrease in the over-dispersion variance (Fig. S6 and S7). The additive genetic, maternal and cohort variances decreased slightly whereas the group variance was similar.

The mean estimate of $V_A(w)$ was slightly reduced, to 0.0149, with a median of 0.0039. The proportion of point-estimates above 0.05 was reduced to 7%, and the 95% confidence interval excluded small values ($V_A(w) > 0.01$) in only 1% of simulations (Fig. S7).

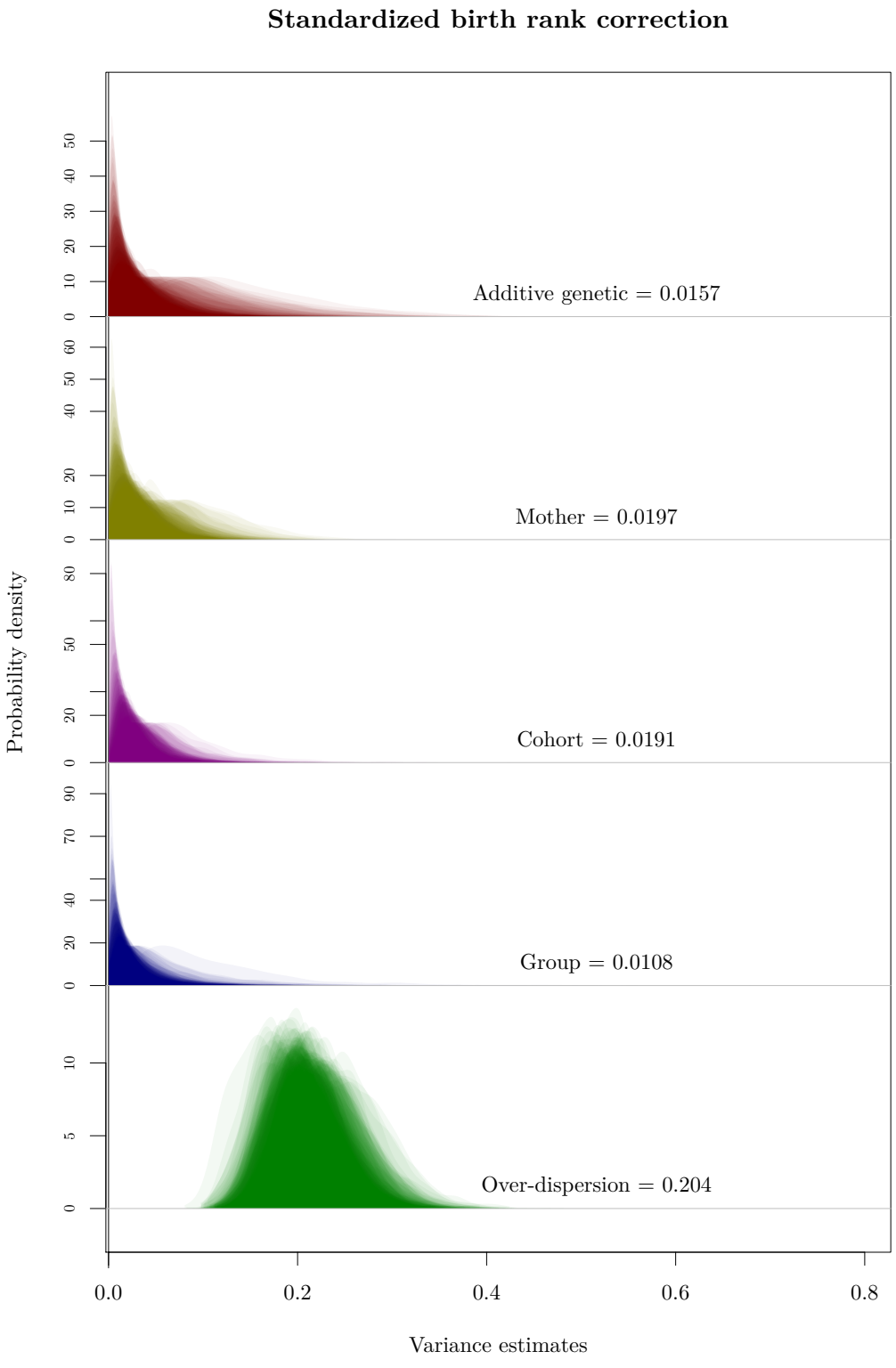

Figure S7: **Posterior distributions of variance components on the data-scale for the 100 simulated spotted hyena datasets when analysed with a correction for social inheritance**. The number on each row are averages of point-estimates among the 100 datasets.

S6 Estimation of $V_A(W)/\bar{W}$

We used a formulation of Fisher's fundamental theorem of natural selection based on the additive genetic variance in relative fitness ($V_A(w)$), which expresses adaptive evolution as a change in relative fitness ($\Delta\bar{w}$) or equivalently as a proportional change in absolute fitness ($\frac{\Delta\bar{W}}{\bar{W}}$). Another common formulation¿ of Fisher's fundamental theorem instead expresses adaptation as a change in units of absolute fitness (ΔW). In this case, the parameter to estimate is the additive genetic variance in absolute fitness, divided by mean absolute fitness ($V_A(W)/\bar{W}$). The two formulations ($\Delta\bar{w} = V_A(w)$ and $\Delta W = V_A(W)/\bar{W}$) are mathematically equivalent but express change on a different scale.

As explained above we reported $V_A(w)$ in the main text, but for completeness we also calculated $V_A(W)/\bar{W}$ parameter for our 19 populations using the most complex model used in each population ("Main model" in table S5 and S4). The results for each population are shown on Figure S8 and are qualitatively similar to results presented on Figure 2 in the main text . The posterior modes varied from 0.003 to 0.87, and $V_A(W)/\bar{W}$ had a meta-analytic average of 0.28, 95%CI $[0.10; 0.55]$. Thus, on average across populations, the response to selection tended to increase mean absolute fitness by 0.28 each generation.

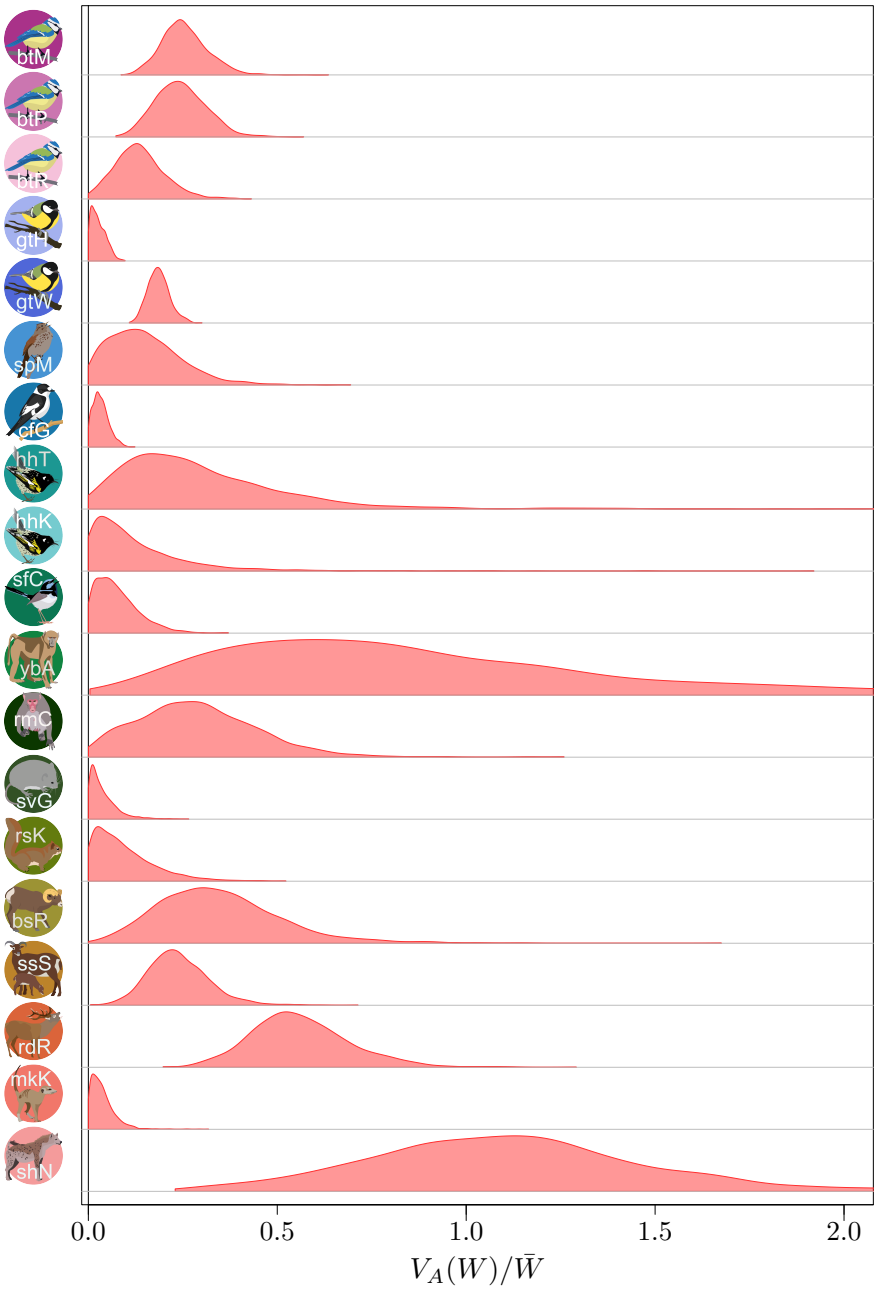

Figure S8: **Posterior distributions of $V_A(W)/\bar{W}$ in each population**. Both $V_A(W)$ and $\bar{W}$ are derived from the most complex model used in each population.

S7 Parameter estimates

In this section, we present several tables with details of parameter estimates from both the population-specific models and the meta-analysis model: a table of population-specific variance-covariance parameters on the link-scales (Table S6), tables of population-specific fixed effect parameters on the link-scale (Table S7), a table of population-specific variance parameters on the scale of the data (Table S9), and a table of meta-estimates of the variance parameters on the scale of the data (Table S10).

Link-scale estimates of random effect variance-covariance parameters

Table S6: Link-scale variance and covariance estimates for random effects in each population. Part P is the conditional-Poisson, part ZI is the zero-inflation, and part Cov is their covariation. These parameters are difficult to interpret because they map to the data-scale in non-linear ways involving interactions with other random effect parameter estimates, fixed effect parameter estimates, and with fixed predictor values.Values in square brackets are 95% Credible Intervals. A "-" indicates the effect was not fitted for a given population.

Popn	Part	Additive genetic	Mother	Cohort	Mother:Cohort	Social	Residual
btM	P	0.000244 [1.54e-07;0.0497]	9.26e-05 [6.19e-09;0.0167]	0.0238 [0.00614;0.0874]	8.31e-05 [3.16e-10;0.0243]	-	0.239 [0.193;0.281]
	Cov	-0.0299 [-0.117;0.0138]	9.91e-05 [-0.0157;0.0196]	0.00504 [-0.122;0.124]	-0.000133 [-0.047;0.0566]	-	0 -
	ZI	0.576 [0.311;0.855]	0.000718 [5.86e-09;0.211]	0.303 [0.105;0.881]	0.383 [0.024;0.77]	-	1 -
btP	P	0.000271 [1.65e-10;0.0581]	0.000195 [1.17e-08;0.0508]	0.000437 [6.9e-07;0.0535]	0.000298 [9.76e-10;0.0525]	-	0.251 [0.196;0.325]
	Cov	0.000199 [-0.0872;0.0636]	2.22e-05 [-0.0273;0.0252]	-0.000575 [-0.0922;0.0545]	-0.00015 [-0.0678;0.0537]	-	0 -
	ZI	0.565 [0.275;0.934]	0.000794 [1.25e-08;0.14]	0.324 [0.132;0.722]	0.00279 [3.69e-06;0.615]	-	1 -
btR	P	8.83e-05 [1.59e-08;0.0221]	0.000104 [4.35e-09;0.0124]	0.0084 [4.85e-07;0.0467]	0.000131 [1.41e-08;0.0279]	-	0.297 [0.263;0.342]
	Cov	-0.000102 [-0.0366;0.0159]	-3.65e-05 [-0.0111;0.0224]	-0.0538 [-0.154;0.0122]	-0.000184 [-0.0193;0.0871]	-	0 -
	ZI	0.127 [4.26e-08;0.284]	0.00105 [3.14e-07;0.209]	0.472 [0.22;1.07]	0.489 [0.258;0.77]	-	1 -
gtH	P	0.000116 [2.28e-09;0.0216]	0.000107 [4.42e-08;0.0207]	0.0216 [0.0106;0.036]	0.0261 [0.0118;0.037]	-	0.344 [0.326;0.369]
	Cov	-2.72e-05 [-0.0277;0.00384]	-1.67e-05 [-0.00757;0.0053]	0.0392 [0.0053;0.0952]	0.00297 [-0.04;0.0387]	-	0 -
	ZI	0.000598 [4.75e-08;0.0981]	7.9e-05 [7.33e-10;0.0223]	0.605 [0.397;0.93]	1.67 [1.51;1.88]	-	1 -
gtW	P	0.0115 [0.0033;0.0168]	2.43e-05 [1.98e-09;0.00745]	0.0258 [0.0171;0.0407]	0.00575 [0.00142;0.0147]	-	0.219 [0.208;0.228]
	Cov	0.12 [0.0616;0.225]	4.48e-05 [-0.0097;0.00818]	-0.0591 [-0.424;0.174]	0.591 [0.156;1.04]	-	0 -
	ZI	9.43 [4.1;10.6]	0.000963 [3.28e-09;0.194]	16.8 [7.66;28.5]	139 [75.7;156]	-	1 -
spM	P	0.000229 [3.26e-11;0.0515]	2e-04 [3.92e-09;0.055]	0.000469 [1.25e-08;0.111]	0.000412 [3.38e-10;0.0563]	-	0.74 [0.574;0.849]
	Cov	0.000257 [-0.0467;0.0569]	-4.04e-05 [-0.0377;0.0241]	0.0131 [-0.0575;0.197]	4e-05 [-0.0841;0.0528]	-	0 -
	ZI	0.00145 [1.11e-07;0.447]	0.000527 [1.87e-09;0.193]	0.634 [0.232;1.34]	0.244 [4.03e-06;0.647]	-	1 -
cfG	P	6.38e-05 [1.07e-09;0.0153]	0.000109 [9.71e-09;0.0197]	0.388 [0.22;0.712]	0.000138 [4.21e-09;0.0379]	-	0.261 [0.225;0.287]
	Cov	3.55e-05 [-0.0212;0.0134]	-2.31e-05 [-0.0111;0.0133]	1.13 [0.573;2.07]	-8.49e-05 [-0.0581;0.023]	-	0 -
	ZI	0.000954 [8.47e-07;0.18]	0.00026 [2.16e-08;0.089]	4.18 [2.42;8.08]	0.516 [0.357;0.682]	-	1 -
hhT	P	0.000597 [4.94e-09;0.0936]	0.000343 [4.22e-08;0.0457]	0.294 [0.0911;1.33]	0.0013 [1.09e-08;0.223]	-	0.599 [0.451;0.814]
	Cov	0.000355 [-0.124;0.0744]	-4.1e-05 [-0.0257;0.0224]	-0.376 [-1.3;0.0229]	-0.000474 [-0.103;0.0639]	-	0 -
	ZI	0.312 [3.99e-08;0.817]	0.000688 [7.65e-09;0.155]	0.95 [0.253;2.64]	0.00161 [2.24e-08;0.283]	-	1 -

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Link-scale estimates of fixed effects

Table S7: Link-scale fixed effect parameter estimates in each population. Part P is the conditional-Poisson (corresponding to parameters for $\boldsymbol{l_2}$ in S1.2), part ZI is the zero-inflation (corresponding to parameters for $\boldsymbol{l_1}$ in S1.2). Note that for the zero-inflation component, a positive effect corresponds to an increase in the proportion of zeroes and therefore a decrease in fitness. Special effects fitted only to some populations are given in another table below, but the parameters presented here are from models including those special effects. Values in square brackets are 95% Credible Intervals.

Population	Part	Intercept	Inbreeding	Sex (male)	Cohort (continuous)	GeneticGrp
btM	P	2.46 [2.16;2.7]	0.889 [-1.29;3.19]	0.0208 [-0.0644;0.133]	-0.086 [-3.38;3.33]	-0.0048 [-0.29;0.249]
	ZI	4.73 [4.02;5.34]	0.579 [-2.49;3.4]	-0.521 [-0.728;-0.35]	-	-0.352 [-0.853;0.41]
btP	P	2.48 [2.15;2.76]	-1.37 [-3.47;2.09]	-0.0848 [-0.203;0.0307]	-1.64 [-4.27;2.21]	0.0318 [-0.336;0.24]
	ZI	3.91 [3.38;4.71]	0.568 [-2.51;3.81]	-0.777 [-1;-0.582]	-	0.481 [-0.239;1.09]
btR	P	2.77 [2.62;2.93]	0.393 [-1.96;2.15]	-0.00981 [-0.105;0.0589]	-1.18 [-4.27;2.26]	0.0192 [-0.15;0.158]
	ZI	3.58 [3.14;4.08]	1.66 [-0.984;4.38]	-0.51 [-0.672;-0.367]	-	0.394 [-0.134;0.804]
gtH	P	2.29 [2.18;2.39]	0.144 [-2.36;1.76]	0.0433 [0.00512;0.0751]	0.354 [-3.27;3.45]	-0.0808 [-0.18;0.0161]
	ZI	3.62 [3.26;3.97]	0.745 [-1.46;3.83]	0.241 [0.183;0.312]	-	0.278 [-0.0997;0.589]
gtW	P	2.35 [2.23;2.43]	-0.805 [-1.59;0.114]	-0.0214 [-0.0371;0.00619]	-0.982 [-4.22;2.4]	0.0426 [-0.0466;0.138]
	ZI	2.43 [0.527;3.46]	5.4 [2.76;8.65]	-0.22 [-0.358;-0.111]	-	9.56 [7.39;10.7]
spM	P	1.81 [1.25;2.47]	-1.38 [-4.01;0.452]	-0.104 [-0.318;0.0492]	-0.52 [-3.59;2.67]	0.843 [-0.0829;1.73]
	ZI	1.52 [0.477;2.73]	5.3 [2.42;7.21]	-0.0297 [-0.259;0.218]	-	0.805 [-0.54;2.32]
cfG	P	1.46 [1.23;1.75]	-0.644 [-2.21;1.58]	0.0713 [0.0314;0.119]	0.146 [-3.17;3.51]	0.0965 [-0.0577;0.247]
	ZI	1.61 [0.781;2.37]	1.05 [-0.982;3.97]	0.0286 [-0.0587;0.107]	-	-0.00377 [-0.341;0.354]
hhT	P	1.54 [1.13;2.01]	-1.57 [-3.46;0.829]	-0.216 [-0.431;6.12e-08]	-1.67 [-4.72;2.07]	0.495 [-0.147;1.45]
	ZI	2.15 [1.43;3.01]	1.55 [-1.29;3.54]	0.412 [0.106;0.656]	-	-1.38 [-2.46;-0.102]
hhK	P	1.79 [1.18;2.5]	-1.08 [-3.61;1.85]	-0.474 [-0.882;-0.144]	-0.85 [-4.14;2.35]	-0.315 [-1.27;0.661]
	ZI	2.26 [1.18;3.35]	1.42 [-1.09;4.66]	0.372 [0.00477;0.854]	-	-1.28 [-2.54;0.0615]
sfC	P	1.87 [1.63;2.14]	0.759 [-2.95;3.35]	-0.354 [-0.497;-0.156]	-0.787 [-4.26;2.36]	0.0614 [-0.165;0.365]
	ZI	3.45 [3.13;3.71]	0.473 [-2.79;3.7]	-1.11 [-1.28;-0.887]	-	-0.21 [-0.573;0.0753]

Population	Parts	Intercept	Inbreeding	Sex	Cohort	GG
ybA	P	0.526 [-0.311;1.12]	0.201 [-3.4;3.44]	-0.641 [-1.32;-0.192]	-1.05 [-3.6;2]	0.134 [-0.27;0.761]
	ZI	2.07 [0.671;3.6]	-0.142 [-3.56;3.12]	1.92 [0.544;3.06]	-	-0.832 [-2.1;1.79]
rmC	P	2.1 [1.91;2.3]	-1.03 [-3.92;2.61]	0.429 [0.282;0.626]	-1.01 [-4.55;1.88]	0.333 [-0.325;0.95]
	ZI	-0.36 [-1.81;0.758]	0.34 [-2.51;4]	1.09 [0.744;1.48]	-	2.77 [2.12;3.66]
svG	P	1.03 [0.676;1.35]	-1.58 [-3.77;1.55]	0.206 [0.00675;0.358]	-0.0471 [-3.98;2.37]	-0.26 [-0.581;0.133]
	ZI	0.273 [-0.699;1.39]	0.432 [-2.71;3.42]	0.866 [0.535;1.33]	-	-1.63 [-2.51;-0.845]
rsK	P	1.87 [1.55;2.06]	1.7 [-1.35;3.85]	-0.963 [-1.22;-0.671]	-0.216 [-3.8;2.47]	0.0443 [-0.3;0.419]
	ZI	2.93 [2.11;3.81]	-1.57 [-3.95;2.63]	0.738 [0.327;1.2]	-	-0.916 [-1.58;0.323]
bsR	P	0.787 [0.165;1.29]	0.016 [-3.08;3.25]	0.0385 [-0.321;0.276]	-0.598 [-3.63;2.67]	0.127 [-0.303;0.681]
	ZI	2.05 [0.897;3.68]	0.215 [-2.69;4.04]	2.87 [2.24;4.2]	-	-3.25 [-4.76;-1.89]
ssS	P	0.183 [-0.382;0.777]	-2.26 [-5.29;0.456]	-0.496 [-0.665;-0.266]	-1.34 [-4.8;1.6]	1.1 [0.538;1.58]
	ZI	2.62 [1.29;4.11]	0.597 [-2.45;3.83]	1.77 [1.33;2.5]	-	-1.78 [-3.01;-0.806]
rdR	P	1.15 [0.901;1.38]	-1.26 [-4.83;0.687]	0.152 [-0.029;0.292]	-4.41 [-7.59;-0.817]	0.35 [0.12;0.695]
	ZI	0.771 [0.0251;1.6]	3.39 [-0.101;6.28]	3.04 [2.56;4.46]	-	-2.15 [-3.11;-1.33]
mkK	P	0.997 [0.553;1.37]	-1.58 [-4.04;0.781]	-0.0713 [-0.341;0.152]	-1.35 [-4.66;1.59]	-0.616 [-1.18;-0.0569]
	ZI	3.16 [2.38;3.87]	-0.000764 [-2.73;3.28]	1.35 [0.965;1.7]	-	-0.82 [-1.68;0.165]
shN	P	1.8 [1.03;2.61]	-0.19 [-3.96;2.67]	-0.424 [-0.76;0.0409]	-0.123 [-0.286;-0.00318]	-0.287 [-0.863;0.662]
	ZI	4.12 [2.19;6.12]	0.536 [-3.12;3.67]	1.59 [-6.33;2.65]	-	-5.72 [-7.11;-0.6]

Notes: btM=blue tits at Muro, btP=blue tits at Pirio, btR = blue tits at la Rouvière, gtH=great tits at Hoge Veluwe, gtW=great tits at Wytham Woods, spM= song sparrows on Mandarte, cfG=collared flycatchers on Gotland, hhT= hihi on Tiritiri Matangi, hhK= hihi at Karori, sfC= superb fairy-wrens in Canberra, ybA= yellow baboons at Amboseli, rmC=rhesus macaques at Cayo Santiago, svG=snow voles in Graubünden, rsK=red squirrels at Kluane, bsR=bighorn sheep on Ram Mountain, ssS= Soay sheep on St Kilda, rdR=red deer on the Isle of Rum, mkK=meerkats in the Kalahari, shN=spotted hyenas in the Ngorongoro Crater.

Table S8: Supplementary social effects fitted for models in the main text.

Population	Effect	Trait	Posterior mode	CI
ybA	average rank	P	-0.84	[-1.59;0.0595]
		ZI	1.63	[-0.539;3.88]
	average rank:sex (female)	P	0.95	[0.0495;1.61]
		ZI	-1.52	[-3.31;0.535]
rmC	medium rank (in females)	P	0.06	[-0.175;0.198]
		ZI	0.22	[-0.262;0.664]
	high rank (in females)	P	0.19	[-0.0239;0.456]
		ZI	-0.27	[-0.801;0.359]
mkK	dominant (yes/no)	P	1.46	[1.22;1.73]
		ZI	-3.68	[-4.17;-3.21]
shN	birth rank relative (female)	P	-0.13	[-0.734;0.389]
		ZI	-0.23	[-2.52;1.09]
	birth rank ordinal (female)	P	-0.01	[-0.0469;0.0151]
		ZI	0.07	[-0.0369;0.176]

Notes: ybA= yellow baboons at Amboseli, rmC=rhesus macaques at Cayo Santiago, mkK=meerkats in the Kalahari, shN=spotted hyenas in the Ngorongoro Crater. For rmC, rank is defined only for females and at the level of the family within a social group. At any given time a group consists of two or three families, and family ranking is determined by the outcome of pairwise agonistic encounters. For mkK, the predictor dominant is binary and indicates whether the individual achieved the status of dominant during their lifetime. Dominant females are responsible for the majority of breeding attempts and dominant males fathers most of the young born to the dominant female.

Back-transformed variance components

Table S9: Data-scale estimates of variance parameters for relative fitness (i.e., back-transformed from the ZI and P linear predictors onto the data-scale; see S2.2.3 for details): the additive genetic variance $V_A(w)$, maternal variance $V_M(w)$, cohort variance $V_C(w)$, maternal:cohort interaction variance $V_{M:C}(w)$ and, in the three populations where it was estimated, social group variance $V_S(w)$. Values are posterior modes and 95% highest posterior density credible intervals.

Population	$V_A(w)$	$V_M(w)$	$V_C(w)$	$V_{M:C}(w)$	$V_S(w)$
btM	0.497 [0.277;0.701]	0.00685 [0.00352;0.164]	0.21 [0.0667;0.8]	0.32 [0.00548;0.65]	
btP	0.492 [0.223;0.677]	0.00687 [0.00371;0.144]	0.279 [0.121;0.762]	0.0351 [0.00352;0.534]	
btR	0.0997 [0.00662;0.21]	0.00624 [0.00328;0.136]	0.493 [0.168;1.12]	0.282 [0.102;0.503]	
gtH	0.0163 [2.12e-05;0.0994]	0.00634 [0.00392;0.0375]	0.326 [0.16;0.518]	1.18 [0.854;1.86]	
gtW	0.0862 [0.0635;0.111]	0.0053 [0.00369;0.0142]	0.31 [0.187;0.536]	2.08 [1.46;3.03]	
spM	0.0624 [0.000226;0.21]	0.009 [0.0034;0.142]	0.223 [0.0684;0.554]	0.148 [0.00316;0.373]	
cfG	0.0182 [0.000164;0.0543]	0.00423 [0.00142;0.0376]	0.429 [0.249;0.727]	0.133 [0.0611;0.229]	
hhT	0.134 [9.82e-05;0.343]	0.0192 [0.00438;0.104]	1.89 [0.451;8.62]	0.0277 [0.00509;0.387]	
hhK	0.0046 [2.46e-07;0.225]	0.0171 [0.00399;0.242]	0.568 [0.0959;3.04]	0.0134 [0.00263;0.191]	
sfC	0.0029 [4.52e-05;0.157]	0.00823 [0.00449;0.107]	0.03 [0.00607;0.147]	0.737 [0.432;1.22]	
ybA	0.231 [0.0314;0.547]	0.0498 [0.00129;0.235]	0.162 [0.0606;0.41]	0.285 [0.128; 0.664]	
rmC	0.117 [0.00115;0.216]	0.0663 [0.00209;0.154]	0.462 [0.234;0.784]	0.0101 [0.00139;0.143]	0.0447 [0.00729;0.141]
svG	0.00462 [2.96e-06;0.0589]	0.00782 [0.000929;0.193]	0.252 [0.123;1.04]	0.00467 [0.000926;0.149]	
rsK	0.0104 [6.36e-05;0.23]	0.0202 [0.00325;0.266]	0.492 [0.27;1.14]	0.472 [0.141;0.988]	
bsR	0.266 [0.0641;0.572]	0.0449 [0.00326;0.367]	0.792 [0.241;2.16]	0.0237 [0.00302;0.212]	
ssS	0.191 [0.0786;0.353]	0.158 [0.0562;0.364]	0.383 [0.198;0.743]	0.439 [0.0337;1.33]	
rdR	0.343 [0.216;0.512]	0.00858 [0.0022;0.163]	0.378 [0.211;0.848]	- -	
mkK*	0.0315 [0.000148;0.27]	0.123 [0.0102;0.358]	0.143 [0.0126;0.528]	0.313 [0.0953;1.04]	0.0857 [0.012;0.485]
shN	0.448 [0.147;0.811]	0.00377 [0.00134;0.139]	0.135 [0.0386;0.383]	0.00491 [0.00138;0.151]	0.00769 [0.00109;0.116]

Notes: *For the Kalahari meerkats (mkK) there was another variance component: litter identity, with a data scale variance parameter estimate of 0.565 [0.095; 2.07]. btM=blue tits at Muro, btP=blue tits at Pirio, btR = blue tits at la Rouvière, gtH=great tits at Hoge Veluwe, gtW=great tits at Wytham Woods, spM= song sparrows on Mandarte, cfG=collared flycatchers on Gotland, hhT= hihi on Tiritiri Matangi, hhK= hihi at Karori, sfC= superb fairy-wrens in Canberra, ybA= yellow baboons at Amboseli, rmC=rhesus macaques at Cayo Santiago, svG=snow

voles in Graubünden, rsK=red squirrels at Kluane, bsR=bighorn sheep on Ram Mountain, ssS= Soay sheep on St Kilda, rdR=red deer on the Isle of Rum, mkK=meerkats in the Kalahari, shN=spotted hyenas in the Ngorongoro Crater.

Meta-estimates of back-transformed variance parameters

After running single models for each population, we combined the 19 estimates of each parameter (variance parameters $V_A(w)$, $V_M(w)$, $V_C(w)$, and proportions of variance (h^2, m^2, c^2) results into a meta-analysis using the Bayesian package brms (*233*) (note that we did not meta-analyse $V_{M:C}(w)$ and $V_S(w)$). For each of these parameters, we report posterior modes and 95% highest posterior density credible interval for two meta-parameters: the meta-average, and the among-populations standard deviation of the parameter (Table S10).

Table S10: Meta-estimates for data-scale variance components and proportions of variance in relative fitness from models reported in the main text.

Variable	Meta-average	Std. Dev.
$V_A(w)$	0.185 [0.0875;0.303]	0.115 [0.00645;0.256]
h^2 (%)	2.99 [0.797;6.9]	1.17 [0.0502;6.55]
$V_M(w)$	0.0716 [0.0298;0.139]	0.0476 [0.00262;0.132]
m^2 (%)	1.13 [0.29;2.47]	0.78 [0.03;2.34]
$V_C(w)$	0.498 [0.254;1.23]	0.253 [0.0137;1.2]
c^2 (%)	7.00 [3.21;13.9]	1.04 [0.0361;9.08]

S8 Application of the evolutionary rescue thought experiment

We applied the evolutionary rescue thought experiment presented in supplementary text S3 above to each of our 19 populations. Given the estimates of $V_A(w)$ observed here for each of the study populations, how many generations would it take for a population to return to, or even exceed, its initial size? We integrated those calculations over the posterior distribution of $V_A(w)$ estimates for each population, to give posterior distributions of the trajectory of population size over generations. We stress this thought experiment is a way to visualise the tendency of a genetic response to selection to increase fitness and is not meant to be a realistic demographic projection. In this thought experiment, in 11 out of the 19 populations the most likely demographic trajectory corresponds to a full recovery from the perturbation in fewer than 10 generations, and population size never goes below 50% of the initial population size (Fig. S9). This is also the most likely trajectory for a hypothetical population with a value of $V_A(w)$ corresponding to the meta-average (of 0.185), in which recovery would occur in 5 generations. In a further two populations (song sparrows, ssM, and meerkats, mkK), recovery takes between 10 and 20 generations, which may or may not be too slow to prevent extinction due to demographic stochasticity, as population size hits a low of 31% (song sparrows) or 9% (meerkats) of the initial size. In contrast, in 6 populations, levels of $V_A(w)$ are so low that adaptive evolution would have no meaningful influence over the course of 10 or even 38 generations (the maximum duration of monitoring in this study). However overall, the results imply that in the majority of our study populations, rates of contemporary adaptive evolution can be sufficiently fast as to be relevant for short-term demographic changes, and by extension for other short-term ecological processes such as trophic networks or nutrient cycles.

In reality, over the study periods, none of the populations showed a clear exponential increase in population sizes such as those produced in the thought experiment (see supplementary text S9 for dynamics of each population). In real populations, adaptive evolution will be far from the only process controlling the dynamics of mean fitness. Genetic changes in fitness can be driven by mutations and gene flow, in particular with the immigration of individuals that are not locally adapted (*240*). In addition to direct genetic changes, various processes of 'environmental deterioration' are likely to take place and counteract any increase in mean fitness in adapting populations (*8, 9, 22*). In particular, when individuals compete for finite resources, such as mates, territories or food, genetic change by natural selection may itself alter the competitive environment in subsequent generations, causing deleterious indirect genetic effects (*11, 24*). Thus, resource limitations always regulate a population and prevent mean fitness from increasing indefinitely (*237, 241*). Finally, continuing environmental change, such as the effects of current anthropogenic climate change, may generate an adaptational lag whereby adaptive evolution is insufficient to fully counter-balance the worsening negative effect of environmental change on mean fitness (*29, 242*). In fact, when a population is essentially stable, high $V_A(w)$ must necessarily indicate, that at least in a very broad sense, substantial environmental deterioration is ongoing.

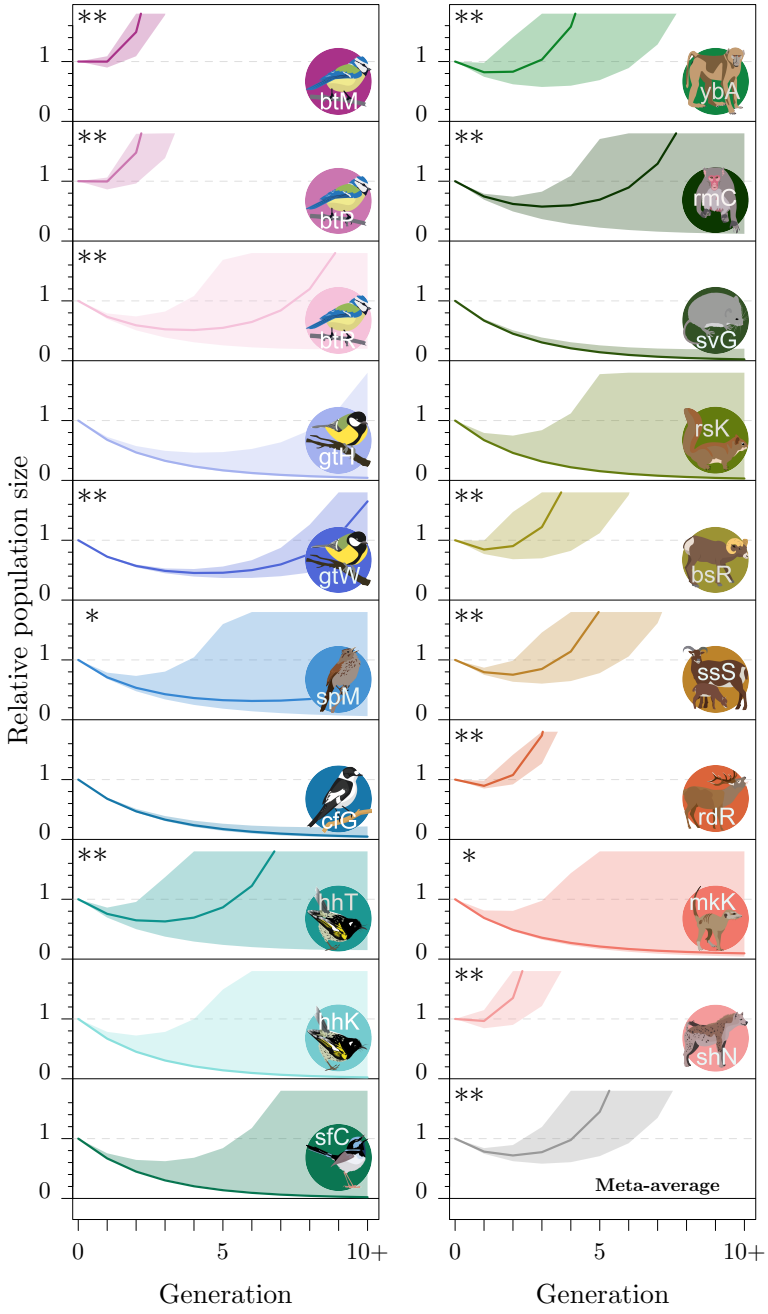

Figure S9: **Hypothetical demographic trajectories for each population following a sudden and permanent environmental change that reduces mean fitness by 1/3 from generation zero, considering effects of adaptive evolution as predicted by estimated $V_A(w)$ in each population**. The final panel shows the trajectory for a hypothetical population with $V_A(w)$ equal to the meta-average. Populations in which the most likely trajectory is a recovery within ten generations are shown with a **, those for which recovery occurs after 11 to 20 generations are shown with a *. This thought experiment illustrates the possible magnitude of adaptation and is not intended as a realistic demographic projection. Thick lines represent posterior modes for population size (relative to starting size) and shaded areas represent 90% credible intervals for each population. The y-axis is truncated at 1.8.

S9 Population dynamics

We present here an overview of the population dynamics of each study population, to illustrate the lack of any clear evidence of exponential growth. Differences in monitoring protocols and data selection between and within populations mean that comprehensive analysis of each population's dynamics is not feasible. For instance, in the tit populations, the number of individuals monitored each year depends heavily on the number of nest boxes installed, and may not exactly reflect the real number of individuals present locally. Also, in mammals, the detection of juveniles that die early in life may vary based on the frequency and intensity of fieldwork. Nevertheless, we present the changes in the number of individuals known in each cohort of each population, to show that none of the populations experienced clear exponential growth over their respective study periods (Fig. S10).

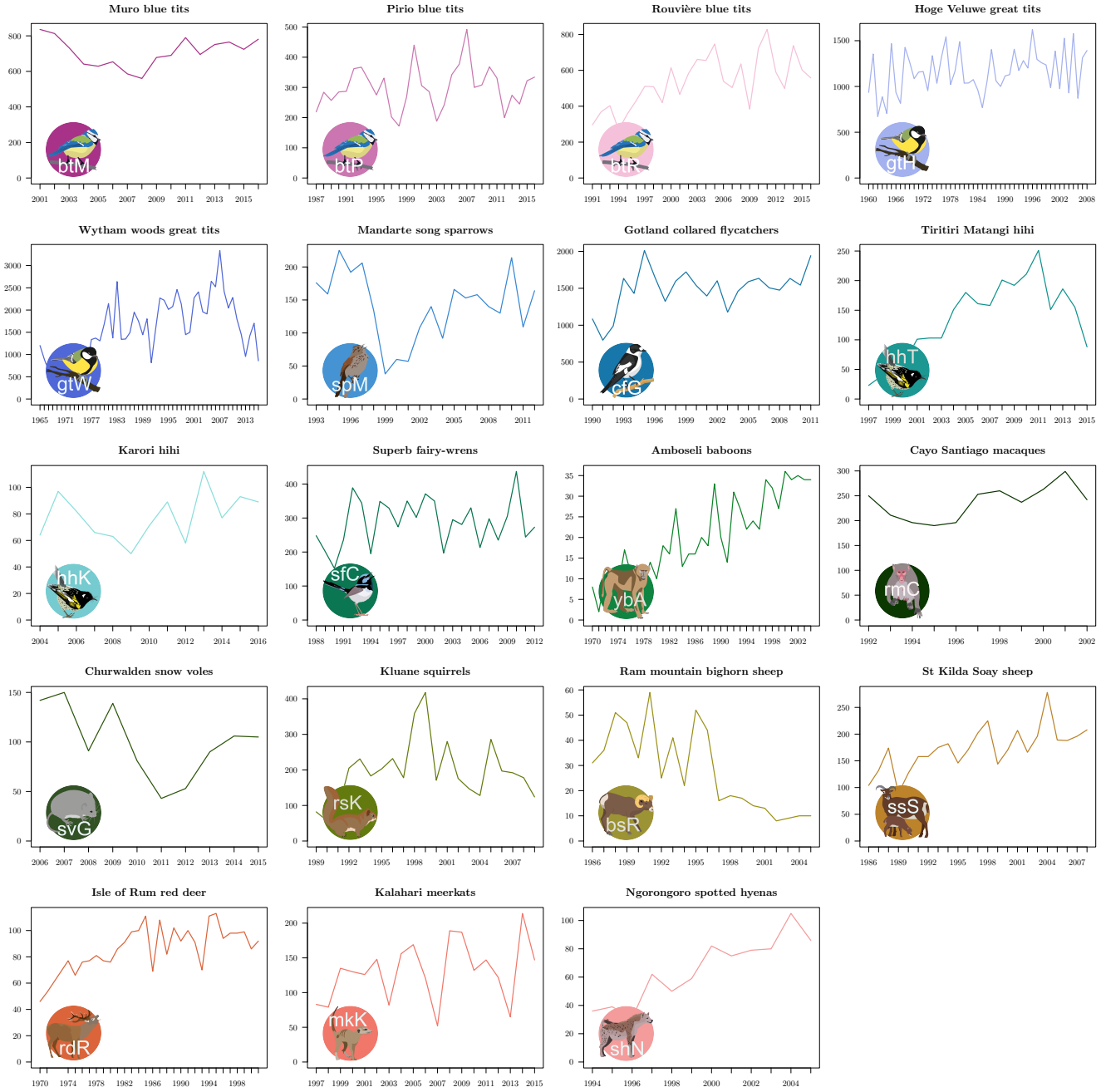

Figure S10: **Dynamics of the number of individuals known in each cohort of each study population**. To exclude the founding phase of each population, only cohorts with at least 50% of individuals with a known parent are shown. Some of the variation in number of individuals comes from changes in sampling protocol and effort. btM=blue tits at Muro, btP=blue tits at Pirio, btR = blue tits at la Rouvière, gtH= great tits at Hoge Veluwe, gtW=great tits at Wytham Woods, ssM= song sparrows on Mandarte, cfG= collared flycatchers on Gotland, hhT=hihi on Tiritiri Matangi, hhK= hihi at Karori, sfC=superb fairy-wrens in Canberra, ybA=yellow baboons at Amboseli, rmC= rhesus macaques at Cayo Santiago, svG=snow voles in Graubünden, rsK=red squirrels in Kluane, bsR=bighorn sheep on Ram mountain, ssS=Soay sheep on St Kilda, rdR=red deer on the Isle of Rum, mkK=meerkats in the Kalahari, shN=spotted hyenas in the Ngorongoro Crater.

S10 Extended acknowledgments

Blue tits; Muro, Pirio and la Rouvière

The blue tit group thanks all researchers and fieldworkers involved in the long-term monitoring over the past 45 years, in particular Jacques Blondel, Samuel Caro, Claire Doutrelant, Marcel Lambrechts, Philippe Perret and Denis Réale; as well as the land owners, the APEEM & GRIPEM associations, and the Vallée du Fango MAB Reserve for facilitating fieldwork.

Great tits, Hoge Veluwe

We thank the board of the National Park de Hoge Veluwe for their permission to work on their property for all these years, the countless people that have been involved in collecting the data and Louis Vernooij for maintaining the data base. Recent genotyping was supported by the ERC (grant StG 202487).

Great tits, Wytham Woods

Recent data collection for Wytham has been provided by grants from Biotechnology and Biological Sciences Research Council (BB/L006081/1), ERC (AdG250164, StG 202487), and the UK Natural Environment Research Council (NERC) (NE/K006274/1, NE/S010335/1).

Song sparrows

We thank the Tsawout and Tseycum First Nations Bands for allowing access to Mandarte Island, and the countless people who contributed to long-term data collection. Funding was provided by the Natural Sciences and Engineering Research Council of Canada to PA, the Swiss National Science Foundation to LFK (recently 31003A-116794) and PN (P2ZHP3_168447 and P400PB_180870), and the European Research Council and the Norwegian Research Council (project 223257) to JMR. The authors declare no conflicts of interest.

Collared flycatchers

The long-term study was funded by a succession of grants from the Swedish Research Council and FORMAS and we are indebted to the numerous people who contributed to data collection and all landowners of our nest box areas.

Hihi; Tiritiri Matangi and Karori

We are very thankful to all staff, students and volunteers who have contributed to monitoring and genotyping of the hihi populations of Tiritiri Matangi Island and Zealandia Sanctuary over the last 20 years. We thank Research England, the New Zealand Department of Conservation and the Hihi Recovery Group for their continued support

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Superb fairy-wrens

We are grateful to the Australian National Botanic Garden for permission to work at the study site and for logistical support. We also thank the many field assistants who contributed to data collection over the years. The monitoring was licensed by the Australian National University Animal Experimentation Ethics Committee. We thank the Australian Research Council for long-term funding of the project, of which the most recent grant for the data in this study was DP150100298.

Yellow baboons

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Rhesus macaques

The Caribbean Primate Research Center, that manages Cayo Santiago, is supported by grant no. 2P40OD012217 from the National Center for Research Resources and the Office of Research Infrastructure Programs of the National Institutes of Health.

Snow voles

Thanks to the many field helpers. The snow vole monitoring was authorized by the Amt für Lebensmittelsicherheit und Tiergesundheit, Chur, Switzerland, and funded by the Claraz-Donation, the Swiss National Science Foundation project grants 31003A_141110 and 31003A_159462/1 awarded to EP, and by the Forschungskredit of the University of Zurich, grant no. FK-16-097.

North American red squirrels

We thank Agnes MacDonald and her family for long-term access to her trapline, and the Champagne and Aishihik First Nations for allowing us to conduct our work within their traditional territory. Grant funding, data collection and project leadership were also provided by Jeff Lane and Ben Dantzer. The Kluane Red Squirrel Project has been supported through grant funding from the Natural Sciences and Engineering Research Council of Canada, the National Science Foundation and Polar Knowledge Canada. We thank the hundreds of field assistants who helped to collect data in the field and Ainsley Sykes for project and data management. Matt Strimas-Mackey provided coding and database support.

Bighorn sheep

We thank the 90+ students, assistants and colleagues who contributed to data collection in the field over 51 years, in particular Jon Jorgenson, Fanie Pelletier, Chiara Feder and Jack Hogg. Alberta Fish & Wildlife provided essential logistic support and access to the field camp. In addition to NSERC of Canada, financial support was provided by the Alberta Conservation Association, the Fonds de Recherche en Nature et Technologie du Québec, The Canada Research Chairs and the Université de Sherbrooke.

Soay sheep

Thanks to the National Trust for Scotland for permission to work on the Soay sheep of St Kilda and to QinetiQ, Kilda Cruises and their predecessors for logistical support. Thanks to everyone involved with Soay Sheep Project over the decades, especially Jill Pilkington, Andrew MacColl, Tony Robertson, Ian Stevenson and Dan Nussey. The core field project has been supported by successive NERC grants (NE/M002896/1), with other support from BBSRC, ERC and The Royal Society.

Red deer

Thanks to NatureScot for permission to work on The Isle of Rum National Nature Reserve, and their staff on Rum for logistical support. Thanks to everybody involved with the red deer project across the decades, in particular to Ali Morris, Sean Morris, Martyn Baker, Fiona Guinness, Steve Albon, Ian Stevenson, Dan Nussey and Craig

Walling. The core field project has been supported by successive NERC grants, with other support from BBSRC, ERC and The Royal Society.

Meerkats

We are grateful to the Kalahari Research Trust and the Kalahari Meerkat Project for access to facilities and habituated animals in the Kuruman River Reserve, South Africa. This paper has relied on records of individual identities and/or life histories maintained by the Kalahari Meerkat Project. This research is part of a project that has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (Grant agreement No. 294494 and No. 742808), the Human Frontier Science Program (funding reference RGP0051/2017) the University of Zurich, the Swiss National Science Foundation and the Mammal Research Institute at the University of Pretoria, South Africa. We would like to thank the Northern Cape Department of Environment and Nature Conservation for permission to conduct the research.

Spotted hyenas

The Ngorongoro Hyena Project thanks the Tanzania Commission for Science and Technology, the Tanzania Wildlife Research Institute, and the Ngorongoro Conservation Area Authority for permission to conduct the study. We also thank all assistants that contributed to monitoring and genotyping of the Ngorongoro Crater spotted hyena population over the past 25 years, in particular P. Naman, K. Wilhelm, D. Thierer, and S. Karl.

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Data S1 caption

The compressed file DataS1.zip contains all data necessary to reproduce the analyses. Decompress it to access one folder for each of the 19 populations: bsR = bighorn sheep on Ram Mountain, btM = blue tits at Muro, btP = blue tits at Pirio, btR = blue tits at la Rouvière, cfG = collared flycatchers on Gotland, gtH = great tits in Hoge Veluwe, gtW = great tits in Wytham Woods, hhT = hihi on Tiritiri Matangi Island, hhK = hihi at Karori, mkK = meerkats in the Kalahari, rdR = red deer on the Isle of Rum, rmC = rhesus macaques at Cayo Santiago, rsK=red squirrels in Kluane, sfC = superb fairy-wrens in Canberra, shN = spotted hyenas in the Ngorongoro Crater, spM= song sparrows on Mandarte Island, ssS = Soay sheep on St Kilda, ,svG = snow voles in Graubünden, ybA = yellow baboons at Amboseli.

Each folder contains a .csv file, containing the phenotypic data, where each row corresponds to an individual and with the following columns:

- LBS, the lifetime breeding success
- inbreeding, the pedigree inbreeding
- Qgg, the expected proportion of immigrant genetic ancestry
- SexU, a variable indicating the sex of the individual (including random assignment for individuals of unknown sex)
- stcohort, a standardized covariate indicating birth year
- id, the individual identifier linked to entries in the inverse additive relatedness matrix
- dam, the identity of an individual's mother
- cohort, the birth year
- DamCohort, the interaction of dam and cohort
- plus potentially other variables to be fitted as fixed and random effects that are specific to each population

This file can be opened in many ways, including in a text editor, in a spreadsheet editor, or in R using the base-R function read.csv().

Each folder also contains a file called Ainv_XXX, where XXX is the population code. This file can be loaded into R using the base-R function load(). It contains the inverse additive relatedness matrix derived from the pedigree using the function MCMCglmm::inverseA() in R, and necessary to fit an animal model. The matrix is most easily used to fit models in MCMCglmm. The dimension names correspond to individuals in the population and are label in a way consistent with the labelling of the column id in the phenotypic data file.

Code S1 caption

The document CodeS1.pdf contains R code to fit the animal models used in this work, back-transform them, and extract critical parameters.