SUPPLEMENTARY INFORMATION

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1 – METHODS

1.1 – Data collection

1.1.1 – Protocol for the classification and status of alien species

Following the ecological frameworks of invasion (Blackburn *et al.* 2011), we define the status of a species with respect to the 3 stages of invasion as follows:

Introduction: a species is considered 'introduced' if released by humans, intentionally or accidentally, in the wild outside its native range at least once. Species described as 'exotic', 'alien', 'invasive', 'introduced', 'naturalized', 'released', 'non-native' or similar are classified as introduced only if they conform to this definition. Introductions to national parks, natural reserves and game parks are included in the dataset if the populations are free ranging and not provisioned. Conversely, introductions into confined environments such as 'ranches', safari parks, captive enclosures, or similar, where animals are food provisioned, are discarded unless animals are subsequently released into the wild or escape from confines. We also ignore any cases where it cannot be confidently determined that an introduction location is outside of the native range, and any unconfirmed introduction (e.g. defined as 'possible' or similar). Moreover, we do not classify as 'alien' those populations that have been reintroduced in areas where the species was formerly present (i.e. within its historical native range). Likewise, records of 'alien' populations that originate from expansion of their range into new areas by their own means (e.g. by natural dispersal as a consequence of climatic changes) are not considered as evidence of introduction. Of a total of 518 species in the main analysis for which all life history traits are available, 172 are classified as introduced following these criteria.

Establishment: within the subset of the introduced mammals, a species is considered successfully established if there is evidence of at least one introduced

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population that is self-sustaining, i.e. a population that successfully reproduces and

2   persists in the wild in a non-native locality for a time interval equal to or greater than

the maximum lifespan of the species, without any form of supplementary care. This

4   temporal interval ensures that an introduced population has had sufficient time to

establish. This protocol is therefore applicable also to cases where an alien

6   population is recorded as 'still present' or 'established' without any specific mention

of successful reproduction. We check the time elapsed from the reported introduction

8   date against the species' longest maximum lifespan as recorded in PanTHERIA

(Jones *et al.* 2009), AnAge (De Magalhaes & Costa 2009), Ernest (2003) and Carey

10   and Judge (2000), or alternative sources if unavailable from these references (full

data reference list in section 4.2). Records of persistence for an introduced

12   population are discarded when time since introduction is less than this time interval.

When the date of introduction is not available, we assess the time interval between

14   the date of publication of the earliest source reporting the presence of the alien

population and its latest recorded presence, and use this as a surrogate for

16   evaluating establishment success of the alien population in the same fashion as

described above. Specifically, if the time interval between publications recording a

18   population as 'established' or 'present' is equal to or greater than the maximum

lifespan of the species, we consider this as evidence of successful establishment.

20   For multiple introductions into the same locality, we calculate the time interval against

which to assess establishment success from the date of the last introduction to the

22   date of the latest recorded presence. We also consider a population successfully

established if there is clear and unambiguous evidence that a species was

24   introduced centuries ago by humans and is still present. Eradications by humans of

alien populations are not counted as failures at this stage if the species has initially

26   established according to the criteria here defined. We discard remaining cases where

no introduction date is available and assessment through date of publication of

28   multiple sources is not possible. Introductions with unknown or uncertain outcomes

are also discarded. Finally, we discard cases of alien populations that originate from

2 continuous releases from fur farms if it is not possible to determine whether a species

is truly established and reproducing in the wild, or whether its presence results

4 exclusively from constant releases. We consider a species as not established if (i)

there is no evidence of at least one introduced population that has established

6 successfully following the criteria here outlined, and additionally (ii) there is evidence

of at least one introduced population that has failed to establish. Of 172 introduced

8 species with all life history traits, 121 are classified as successful and 28 as

unsuccessful at establishment stage following these criteria; for 23 introduced

10 species the outcome of their introductions is uncertain and are therefore excluded

from the analysis at establishment and spread stages.

12 <u>Spread</u>: within the subset of successfully established mammals, a species is

classified as successful at spread if at least one established population exhibits

14 remarkable range expansion from the initial location of introduction (van Kleunen *et al.* 2010a; 2010b; Blackburn *et al.* 2011). Words such as 'widespread', 'common',

16 'expanding', 'flourishing', 'invasive', 'pest', or similar are considered evidence of

successful spread if in conjunction with detailed description of range and/or

18 population expansion. Populations that are described, as 'restricted', 'not expanding

beyond the location of introduction' or similar, or populations with very limited range

20 expansion, are classified as unsuccessful at this stage. Cases of range expansion

across small islands (<50,000km^2) are discarded as we consider the available area

22 too small to adequately assess success at spread as defined above; however, we

consider lack of spread within small islands as evidence of failure to spread. Species

24 classified as unsuccessful at spread are therefore those for which none of the

established populations, with sufficient information and not introduced on small

26 islands, exhibits remarkable range expansion. For cases where wording associated

with success at spread, as described above, is only mentioned in brief descriptions

without any supporting evidence in the original source, we look for further evidence of

2 substantial range expansion from additional sources (section 4.2) and use any

qualitative information in the same fashion as described above. When recent maps of

4 the extent of invaded range are available we use these to resolve, confirm, or update

original records on whether range expansion is remarkable given the date of

6 introduction. Typically this leads to confirming the qualitative description or provides

information where none is available in the original source. All ambiguous cases are

8 thoroughly investigated and classified independently by at least two authors. All

these contentious cases are then discussed and, if the information is still insufficient

10 to make a decision or not available, we discard the original record from the dataset

as no judgement can be made with confidence. For a few species where no decision

12 can be reached on the success at spread for any of its alien populations, the species

are excluded from the dataset of species at stage of spread (but retained for the

14 analyses at introduction and establishment as no ambiguity is present at those

stages). Of the 121 established species with all life history traits, 47 are classified as

16 successful at spread and 27 as unsuccessful, while 47 species are excluded from the

analysis at this stage due to lack of sufficient information (i.e. of all established

18 populations across all species that are discarded: approximately 65% are on small

islands; less than 1% are excluded due to post-establishment eradication; about 8%

20 have insufficient data and for about 25% no additional information is available).

Using this protocol, we extract data on invasion success from three main sources

22 (Long 2003; DAISIE 2008; IUCN 2013) complemented by additional sources (full

data reference list in section 4.2). To ensure that our classification at both the

24 population and the species level is robust and objective, all records and information

for 10% randomly selected species and all the critical records that determine the

26 outcome at spread of all the successfully established species were double checked

by at least two authors. Moreover, at least two authors double-checked all

information regarding all ambiguous cases in the original source for all stages of

2 invasion, and the classification resulting after additional checks and information are

found (if available); for cases where a decision cannot be made at a stage,

4 ambiguous records are discarded. Where necessary, we update species' names to

match the taxonomy of Wilson & Reeder (Wilson & Reeder 2005).

6 **1.1.2 – Classification of alien mammals at the species level**

Here we are interested in investigating whether a species has the potential to invade

8 and exhibits preadaptations that promote its success in novel environments, rather

than in explaining which characteristics of the introduction sites or receiving

10 communities explain the success of alien populations. Thus, although success at a

stage is a population level event, we consider one successful event (i.e. one alien

12 population) as sufficient evidence to demonstrate that a species, as a whole, has the

potential to succeed at that stage. In support of this approach, studies on invasive

14 species at smaller geographical scales demonstrate that 'success elsewhere' is a

very strong predictor of success of newly introduced alien populations of the same

16 species in a novel region. For example, while controlling for introduction effort, a

history of successful invasion elsewhere in the world is a strong predictor of

18 establishment success in mammals and birds introduced to Australia, reptiles and

amphibians introduced to California, Florida and Britain, and alien fish in California

20 (Duncan *et al.* 2001; Forsyth *et al.* 2004; Marchetti *et al.* 2004; Bomford *et al.* 2009),

and alien plants (Kolar & Lodge 2001). Furthermore, Forsyth *et al.* (2001) show that,

22 after controlling for introduction effort, within species variation in outcomes across

locations for ungulate and bird species introduced to New Zealand is explained by

24 unsuitable habitats at the introduction location. Similar results have been found in

plants (Richardson & Pyšek 2012). Finally, in taxonomically based studies using

26 success/failure at the event (i.e. population) level ranked within species, species

identity is one of the strongest predictors of success (e.g. Tingley *et al.* 2011; Rago *et*

al. 2012; Sol *et al.* 2012). Altogether this evidence strongly suggests that a species

2   classification for success is justified and appropriate when investigating species'

    potential to invade, as successful invaders in one location are more likely to succeed

4   than to fail in other locations, and failures at one location of successful invaders

    elsewhere are most likely explained by introductions to unsuitability of habitats and

6   low introduction effort.

    Several studies on invasive species model success as a location level event

8   nested within species, but mostly either ignore (i.e. analyses without phylogeny),

    overestimate (e.g. with independent contrasts) or underestimate (e.g. using

10 taxonomy as a proxy of phylogeny) species' similarity due to shared ancestry. Here

    we use novel phylogenetic comparative approaches for binary dependent variables

12 to quantify the phylogenetic signal in the data (Hadfield 2010). In phylogenetic

    comparative analyses across species, the species is the unit of analysis and

14 individual events of introduction for the same species are modeled as intraspecific

    variation, treated as a random effect (Hadfield 2010). However, simulations and

16 empirical analyses demonstrate that within species variation in phylogenetic

    comparative analyses only slightly improves parameter estimates and the estimate of

18 the phylogenetic signal, but crucially it does not alter either the direction or the

    significance of model parameters for the fixed effects (Ives *et al.* 2007; Revell &

20 Graham Reynolds 2012). Thus, including event level outcomes at a stage for every

    species with multiple introductions in our analyses would not alter our conclusions,

22 particularly when also considering that life history traits would not vary across

    locations for a species. Conversely, such an approach would heavily reduce sample

24 sizes of species by up to 40% due to missing data on the outcomes of individual

    introductions (see below) and consequently the power of the analyses.

26 Specifically, including event level outcomes for a species to be modeled as within

    species variation would require that a different measure of introduction effort is used,

as number of locations would no longer be applicable (since locations would be

2 modeled as within species variation). Therefore, a location level approach would

require that introduction effort is estimated as number of introduced individuals for

4 each alien population. There is however no information or only qualitative information

on number of introduced individuals for approximately 75% of the recorded

6 mammalian introductions in our dataset. This will have two major consequences,

namely: (i) the extent of within species variation would be much reduced with

8 approximately 40% of species having data for only one alien population, and (ii) the

sample size of species would be reduced by about 40% at establishment and 30% at

10 spread, compromising greatly the power of analyses aiming to test all the life history

traits and introduction effort in a single model.

12   Conversely, our approach to classify a species as successful at a stage if at least

one of its alien populations has succeeded at that stage allows us to: (i) use all

14 available information about the status of alien populations for a species, regardless of

whether information on the number of introduced individuals is available (see also

16 section 1.1.3 for how we control for introduction effort); (ii) have a large and sufficient

sample of species to test the predictions of the two opposing theoretical models on

18 population growth (Pimm 1991; Sæther *et al.* 2004) at both establishment and spread

while quantifying the relative effect of each life history traits on success (and so

20 account for the correlated evolution between life history traits; see section 1.2.2); and

(iii) account for the phylogenetic signal in the data as estimated by the model

22 (Hadfield 2010). Our approach is supported by independent evidence that successful

species in one location are more likely to succeed in other locations, that failed

24 introductions of successful species are mostly caused by habitat unsuitability, and

that species identity is a strong predictor of success. Our approach is also justified by

26 independent studies showing that parameter estimates and the significance of the

fixed effects in phylogenetic comparative analyses are qualitatively unaltered when

2   within species variation is included.

1.1.3 – Introduction effort

4   It is well established that higher introduction effort (also called 'introduction pressure'

or 'propagule pressure') strongly increases the chances of successful establishment

6   (Cassey *et al.* 2004; Lockwood *et al.* 2005; Simberloff 2009; Sol *et al.* 2012). Ignoring

this factor can lead to erroneous conclusions in comparative analyses on the

8   determinants of invasion success across species (Cassey *et al.* 2004). The

magnitude of introduction effort is dependent on the number of introduced individuals

10   and introduction events to the same locality, and the number of unique introduction

locations (Lockwood *et al.* 2005; Simberloff 2009; Blackburn *et al.* 2011). These

12   factors are positively associated with one another, and they all increase the

probability of a species to successfully establish; species that are introduced in larger

14   numbers, more frequently, and in more locations have higher chances to establish in

non-native regions (Duncan *et al.* 2001; Forsyth & Duncan 2001; Cassey *et al.* 2004;

16   Forsyth *et al.* 2004; Lockwood *et al.* 2005; van Wilgen & Richardson 2012).

Moreover, studies on the establishment success of alien mammals (Forsyth *et al.*

18   2004) and birds (Duncan *et al.* 2001) in Australia show that the number of unique

locations of introduction is as strong (or better) a determinant of success as the other

20   two factors.

We extract data on the number of unique introduction locations from the sources

22   reporting the status of alien mammals (Long 2003; DAISIE 2008; IUCN 2013) (see

also section 4.2). We count repeated introductions to the same unique locality as one

24   introduction location, but multiple localities in the same region or country as unique

introduction locations. When detailed information is not available and a species is

26   reported as being introduced to a region, we adopt a conservative approach and

count the whole region as one introduction location. For example, Guinea pigs (*Cavia*

porcellus) have been introduced to New Zealand but no further details are reported

2   (Long 2003); we thus count this as one introduction location. Conversely, axis deer

(*Cervus axis*) are introduced to multiple named locations and islands of New

4   Zealand; we count these as separate introduction locations (Long 2003).

For approximately 25% of the recorded introductions across all species in our

6   dataset, the number of introduced individuals is also known. For each species we

thus record the total number of introduced individuals across all introduction locations

8   (Sum individuals), and the largest number of introduced individuals in a single

location (Largest introduction). As in previous studies in mammals and birds at small

10   geographical scale (Duncan *et al.* 2001; Forsyth & Duncan 2001; Cassey *et al.* 2004;

Forsyth *et al.* 2004), we find that the number of introduction locations (N locations) is

12   strongly and positively associated with the number of introduced individuals across

species at the global scale, regardless of how the number of introduced individuals is

14   quantified (Pearson's correlation for: N locations vs Sum individuals r=0.78,

T_{88}=11.71, p<0.001; N locations vs Largest introduction: r=0.69, T_{88}=8.96, p<0.001).

16   These results, together with the fact that the number of introduction locations is a

strong predictor of success regardless of how we analyse it (see Section 2.4),

18   demonstrate that the number of introduction locations is a very good estimate of the

magnitude of introduction effort across species. Therefore, following previous studies

20   (Duncan *et al.* 2001; Forsyth *et al.* 2004; Krivánek *et al.* 2006; van Wilgen &

Richardson 2012), we use the number of unique locations of introduction as an

22   estimate of introduction effort to maximize sample sizes, since other measures of

introduction effort are available for fewer mammals in our dataset.

24   **1.1.4 – Offspring value index (OV)**

We calculate an 'offspring value' (OV) index as a measure of current versus future

26   reproductive effort following previous studies (Bókony *et al.* 2009; Sol *et al.* 2012) as:

Equation 1: $OV = \dfrac{1}{(Litters\ per\ year) * (Reproductive\ Lifespan)}$

2   Recent theoretical models of how small populations overcome extinction risks in

variable environments propose that longer lived species are more likely to succeed

4   and establish than shorter lived, highly fecund species (Sæther *et al.* 2004; Jeppsson

& Forslund 2012). Relative to short lived species, long lived organisms can adopt

6   more flexible strategies, such as bet-hedging, when facing temporally and/or spatially

heterogeneous or stochastic environments. Specifically, they can postpone

8   reproduction in unfavourable years and invest into a greater reproductive output in

more favourable years. In the context of these models, a low OV is predicted to be

10   associated with higher probability of establishment of alien populations and so the

association between success and OV should be negative (Sol *et al.* 2012). A recent

12   study in birds finds support for this model and reveals that a low OV can be achieved

through a variable combination of clutch size and lifespan (Sol *et al.* 2012).

14   Specifically, successfully established alien birds with low OV produce either many

clutches per a year over short reproductive lifespan or a single annual clutch over a

16   long reproductive life. This study also shows that OV in birds is unrelated to other life

history traits, suggesting that OV captures an independent dimension of the species'

18   life history strategy (Sol *et al.* 2012).

     Here we assess the relationship between OV and life history traits (section 2.2) to

20   investigate whether OV represents an independent life history axis in mammals, as

suggested for birds (Sol *et al.* 2012).

22   **1.2 – Statistical analysis**

    1.2.1 – Estimating the effect sizes for the life history variables: average partial

24   **effects (APEs)**

    We use average partial effects (APEs) as a measure of the effect size of the

26   continuous life history traits (Long 1997; Greene 2012) that have been identified as

influential in the main analysis. APEs are estimates of the probability of change in the

2 response variable (from 0 to 1 and *vice versa*) for a unit change in a given

independent variable, averaged across all observed values of all independent

4 variables in the model (Long 1997; Greene 2012). For each independent variable we

derive the posterior distributions of its APE from the posterior distributions of its β

6 estimates, i.e. we estimate the APE for every iteration of the posterior β values, using

the following equation (Greene 2012):

8 **Equation 2**: $APE \ of \ x_c = \sum_{i=1}^{n} \frac{f(x_i'\hat{\beta})\widehat{\beta_c}}{n}$

Where f is the normal density function (ϕ) for a probit model, $\widehat{\beta_c}$ is the parameter

10 estimate of a continuous independent variable x_c, $(x_i'\hat{\beta})$ are the fitted model values

for each independent variable, and n is the number of observations. At a single

12 iteration, Equation 2 quantifies the contribution of the parameter estimate $(\widehat{\beta_c})$ for a

continuous independent variable (x_c) to the fitted model values $(x_i'\hat{\beta})$ at every

14 observed value of all other independent variables in the model, and therefore

estimates the average partial effect of x_c at that iteration (Mood 2010). In a Bayesian

16 framework, APEs are calculated at each iteration of the posterior distribution of

estimates, resulting in a posterior distribution of APEs for each independent variable.

18 **1.2.2 – Robustness of the results to multicollinearity**

Some life history traits covary in mammals along at least two life history axes (Bielby

20 *et al.* 2007). Therefore we assess whether possible multicollinearity between all the

predictors (i.e. life history traits and introduction effort where appropriate) in our

22 models has any effect on our conclusions.

Variance inflation factors (VIF) are commonly used to quantify how much the

24 variance of a given parameter is increased in the presence of multicollinearity (Quinn

& Keough 2007). We calculate VIFs for all life history traits from non-phylogenetic

2   GLS regressions. This is a conservative approach since it is well established that the

strength of the associations between life history traits is weakened once phylogeny is

4   accounted for, and therefore VIFs are likely to be higher in a non-phylogenetic

analysis than in a phylogenetic comparative analysis accounting for species' shared

6   ancestry. VIFs are calculated as:

Equation 5: $VIF_k = \dfrac{1}{(1 - R_k{}^2)}$

8   where $R_k{}^2$ is the R^2 value obtained by regressing the kth predictor on the remaining

predictors. VIF values greater than 5 are considered evidence of possibly

10   problematic collinearity and greater than 10 of strong collinearity (Quinn & Keough

2007).

12   When we find evidence of possibly problematic multicollinearity in a model, we

first remove the life history variable with the highest VIF value from the model. We

14   then recalculate VIFs for the new reduced model, and if any remaining variable has a

VIF greater than 5, repeat the procedure until all remaining variables have VIFs lower

16   than 5. We call these models 'reduced models' as they contain only the subset of life

history traits with VIFs lower than 5. We then repeat the analyses of probability of

18   success at each stage of invasion in MCMCglmm (with the same specifications as

the main analysis, as described in the main text) with these 'reduced models' and

20   assess the relative contribution of each independent variable as described in

sections 1.2.1.

22   In section 2.1 we report the VIFs for all life history variables and introduction effort

in the full and reduced models, and the results of the reduced models (mean and SD

24   of the posterior distribution of β estimates for each remaining independent variable in

the reduced models and percentage of their posterior distribution crossing zero; for

2   details on the methods see main text and 1.2.1).

1.2.3 – Associations between offspring value index and life history traits

4   We assess whether the offspring value index (OV, see 1.1.3) exhibits any association

with each life history trait individually using phylogenetic generalized linear models in

6   MCMCglmm (Hadfield & Nakagawa 2010). We use normally distributed priors with a

mean of 0 and a large variance around the mean (10^8) for the life history traits

8   treated as fixed effects (Hadfield & Nakagawa 2010; Hadfield 2012), and a proper

Cauchy prior with wide scaling variance (10^8) for the phylogeny treated as a random

10   effect (Hadfield & Nakagawa 2010; Hadfield 2012). The MCMC chains are run as

described in the main text. This analysis is repeated for each stage of invasion. Here

12   we report the mean and SD of the posterior distribution of β estimates for the slope of

the pairwise association between OV and each life history traits, and the percentage

14   of the β posterior distribution crossing over 0 (main text).

1.2.4 – Potential sampling biases

16   The dataset for the main analysis includes mammals for which data on *all* life history

traits are available (n=518, introduction stage; main text and section 1.1.1). We

18   assess potential sampling biases with regard to life history traits by checking whether

our total sample of species for the main analysis is a random sample from across the

20   mammalian phylogeny. To do so we test if the mean values of each life history trait

differ between mammals in the dataset for the main analysis (with all life history data;

22   'Included' sample, n=518) and mammals that lack data for at least one life history

trait ('Excluded' sample). We thus code each mammalian species as either 'included'

24   or 'excluded' in the dataset for the main analysis and perform a phylogenetic t-test in

maximum likelihood within PGLS in BayesTraits (Pagel *et al.* 2004), with the life

26   history trait of interest as the dependent variable, and the classification of the species

as 'Included' in the main analysis (coded as 1) or not (coded as 0, i.e. 'Excluded-all'

2   sample) as independent binary variable.

2 – SUPPLEMENTARY RESULTS

4   **2.1 – Multicollinearity: variance inflation factors (VIF) and reduced models**

Some life history traits in the full model (with all the independent variables) have VIFs

6   greater than 5 (Table S1). According to the protocol described in section 1.2.2, we

exclude the following variables from the models: neonatal body mass and age at first

8   birth for introduction, neonatal body mass for establishment, and neonatal and adult

body mass for spread. The VIF values of all the independent variables retained in

10   these reduced models are below 5, indicating that multicollinearity is no longer

potentially problematic (Table S1).

12   Next we re-run the analyses on the probability of success at each invasion stage

with only the independent variables retained in the reduced models, with the same

14   model specification as the full models (see main text and section 1.2.2). These

produce qualitatively similar results to those presented in the main text (full models;

16   Tables S2). Specifically, we find again strong effects of larger litter size, more litters

per year and longer reproductive lifespan on the probability of being introduced in

18   non-native environments (Tables S2a). Thus, the APEs (section 1.2.1) indicate that

the relative probability of being introduced increases by approximately 3.9% for every

20   additional offspring produced in a litter, 2.0% for every additional litter produced per

year, and 3.9% for every additional day of reproductive lifespan (Table S2a). At

22   establishment, litter size, reproductive lifespan and introduction effort are influential

on the probability of success (Table S2b), such that every additional offspring

24   produced increases the relative probability of establishing by 3.8% and a day longer

reproductive lifespan by 1.8% (Table S2b). At spread, larger and more frequent

26   litters, and higher introduction effort increase the probability of success at this stage

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as in the main analysis, but we also find a weaker effect of older weaning age

2   (Tables S2c). Consistent with the main analysis (main text, Figure 1b), the relative

probability of successfully spreading into non-native regions increases of 3.8% and

4   5.2% for every additional litter produced in a year and every additional offspring in a

litter respectively, and 3.0% for every additional day of lactation (Table S2c).

6   Altogether this analysis confirms our main result that introduced species produce

larger and more frequent litters over a longer reproductive lifespan; greater

8   introduction effort, larger litters and longer reproductive lifespan increase the

probability of success at establishment, while success at spread is associated with

10   higher productivity, greater introduction effort and possibly with marginally longer

postnatal maternal investment (Tables S2). The heritability values are qualitatively

12   similar between the full (main text, Figure 2a) and reduced model (Figure S1).

1 **Table S1**. Variance inflation factors (VIF) of the independent variables in the full models and the reduced models at each invasion stage (introduction,

2 establishment and spread). Values of VIF greater than 5 are considered potentially problematic (see section 1.2.5 for details). The independent variables in

3 the table are reported as follows: adult body mass (BM), gestation time (GT), weaning age (WA), neonatal body mass (NBM), litter size (LS), litters per year

4 (LY), age at first birth (AFB), reproductive lifespan (RL), introduction effort (IE). For the reduced models 'NA' indicate that a given independent variable has

5 been excluded from the models due to its high VIF value in the full model.

Invasion stage	Introduction		Establishment		Spread	
VIF for:	Full model	Reduced model	Full model	Reduced model	Full model	Reduced model
BM	8.45	3.29	6.99	3.88	9.19	NA
GT	9.38	4.34	11.88	3.07	15.41	3.00
WA	3.27	2.82	3.78	3.05	5.14	3.60
NBM	12.99	NA	14.79	NA	20.86	NA
LS	2.88	2.78	3.42	3.13	3.34	3.32
LY	3.32	2.62	2.87	2.76	2.43	2.30
AFB	5.08	NA	3.42	3.35	2.63	2.43
RL	3.52	3.28	2.84	2.82	2.74	2.62
IE	NA	NA	1.22	1.22	1.33	1.14

1 **Table S2.** Comparison of the results between the full model (with all life history traits, as
2 presented in the main text; left columns in this table) and the reduced models (where some
3 life history variables have been excluded after controlling for multicollinearity, right columns,
4 see Table S1). For each independent variable we report the mean and SD of the β posterior
5 distribution, and the percentage of β posterior distribution (% β) beyond zero (see main text
6 for details). Stages of invasion: in (a) introduction, in (b) establishment, and in (c) spread. The
7 independent variables in the table are reported as follows: introduction effort (IE), adult body
8 mass (BM), gestation time (GT), weaning age (WA), neonatal body mass (NBM), litter size
9 (LS), litters per year (LY), age at first birth (AFB), reproductive lifespan (RL). For the reduced
10 models 'NA' indicates that a given independent variable was not included.

(a) Introduction	Full model			Reduced model		
Statistics	Mean β	SD β	% β	Mean β	SD β	% β
BM	0.38	0.41	17.1	0.12	0.22	28.1
GT	-0.77	1.02	22.1	-1.06	0.89	11.3
WA	0.03	0.54	46.7	0.12	0.52	40.7
NBM	-0.38	0.49	20.4	NA	NA	NA
LS	2.91	0.91	0.0	3.01	0.83	0.0
LY	1.66	0.75	1.0	1.52	0.69	1.4
AFB	0.25	0.58	33.6	NA	NA	NA
RL	2.99	0.74	0.0	3.00	0.71	0.0

(b) Establishment	Full model			Reduced model		
Statistics	Mean β	SD β	% β	Mean β	SD β	% β
BM	-0.30	0.85	36.0	-0.18	0.57	38.3
GT	-2.20	2.41	17.5	-1.94	1.81	12.8
WA	0.90	1.41	26.0	0.82	1.31	25.8
NBM	0.15	0.97	42.9	NA	NA	NA
LS	5.51	2.70	0.9	5.23	2.61	0.8
LY	1.44	2.21	25.9	1.41	2.13	25.4
AFB	0.61	1.62	34.9	0.59	1.58	34.8
RL	2.49	1.92	8.9	2.39	1.85	8.9
IE	2.70	0.85	0.0	2.61	0.82	0.0

2

(c) Spread	Full model			Reduced model		
Statistics	Mean β	SD β	% β	Mean β	SD β	% β
BM	0.28	0.85	36.3	NA	NA	NA
GT	-0.54	3.28	43.1	-0.58	1.83	38.1
WA	1.96	1.83	13.8	2.10	1.63	9.1
NBM	-0.23	1.11	42.5	NA	NA	NA
LS	3.93	2.30	3.7	3.70	2.07	2.6
LY	3.15	2.39	8.2	2.79	2.16	8.3
AFB	1.55	1.53	15.4	1.36	1.35	15.4
RL	0.31	1.84	43.1	0.33	1.59	41.4
IE	1.77	0.82	1.0	1.72	0.74	0.6

4
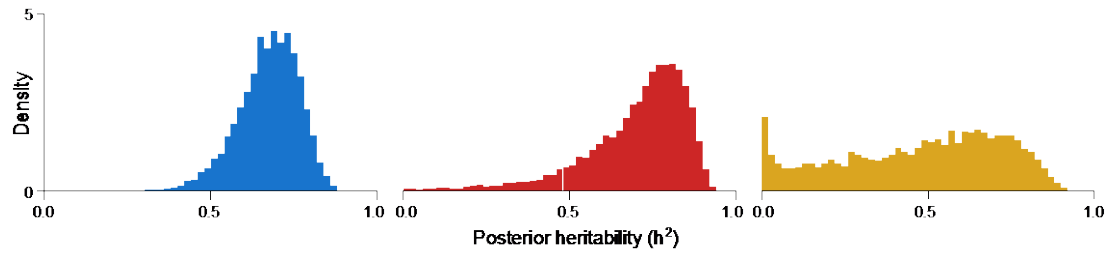
2   **Figure S1.** Posterior distribution of heritability (h^2) at introduction (blue),

establishment (red) and spread (yellow) for the reduced model in which

4   multicollinearity is resolved.

6   **2.2 – Offspring value and life history traits**

The offspring value index (OV) has been proposed and used as an estimate of

8   current versus future reproductive investment in previous studies (Bókony *et al.*

2009; Sol *et al.* 2012) (see main text and section 1.1.3). In birds this index is

10   unrelated to life history traits, suggesting that it represents another life history axis in

this lineage (Sol *et al.* 2012). In mammals, however, we find that low OV (indicating

12   that reproductive investment is divided in more reproductive attempts during the

reproductive lifespan of a species) is associated with larger litters, fewer litters per

14   year, faster life history traits and smaller body mass, at all stages of invasion (Table

S3). These findings, together with the results showing stronger associations between

16   life history traits and success at each invasion stage (main text) relative to those

found with OV (main text), suggest that the importance of OV for success at

18   introduction (main text) reflects the fact that OV is not an independent life history axis

in mammals and conversely that these results reflect the associations of OV with the

20   life history strategy of a species.

22   **Table S3.** Pairwise phylogenetic generalized linear model between offspring value

index (OV) and each life history trait (LH) at each stage of invasion. We report the

mean and SD of posterior distribution of β estimates for the slope of the association

2   between OV and each life history trait, and the percentage of β posterior distribution

crossing over 0. Variable names: BM (adult body mass), GT (gestation time), WA

4   (weaning age), NBM (neonatal body mass), LS (litter size), LY (litters per year), AFB

(age at first birth), RL (reproductive lifespan).

Stage	Introduction			Establishment			Spread		
LH	Mean β	SD β	% β	Mean β	SD β	% β	Mean β	SD β	% β
BM	-0.05	0.02	0.0	-0.08	0.03	0.3	-0.13	0.04	0.0
GT	-0.12	0.07	5.0	-0.30	0.10	0.2	-0.47	0.17	0.3
WA	0.02	0.04	30.8	-0.01	0.08	44.1	-0.18	0.12	6.0
NBM	-0.08	0.02	0.0	-0.11	0.03	0.1	-0.16	0.04	0.0
LS	0.26	0.07	0.0	0.41	0.10	0.0	0.31	0.18	4.2
LY	-0.79	0.06	0.0	-0.87	0.11	0.0	-0.66	0.17	0.0
AFB	0.01	0.04	37.6	0.10	0.08	9.8	-0.02	0.10	42.8
RL	-0.89	0.04	0.0	-0.93	0.08	0.0	-0.85	0.08	0.0

6

2.3 – Potential sampling biases

8   We assess whether there are biases in the total pool of species used in the main

analysis (n=518) and compare this pool ('Included' species, see main text) with

10 mammals for which at least one life history trait is missing ('Excluded' species

sample; sections 1.1.4). The phylogenetic t-tests show that there are small biases in

12 the sample of species for which we have all available life history data. Species

included in our dataset for the main analysis ('Included' sample) differ from the

14 'Excluded' species in three life history traits: body mass, litter size, and reproductive

lifespan (Table S4). However, the β values for such differences are small, particularly

16 when considered in the light of the large sample sizes of this analysis (Table S4).

Table S4. Phylogenetic t-test in PGLS on the mean values of each life history trait
between the sample of species used in this study ('Included', n=518, main text) and
those excluded ('Excluded', section 1.2.4). The sample size of the species excluded
from our analysis ('Excluded') varies for each life history trait tested. Here we report
the total sample size for this analysis (included and excluded species together, 'N
total'), the sample size of the 'Excluded' sample ('N Excluded'), and the t-value, p-
value and strength of the phylogenetic signal, as quantified by the λ parameter in
PGLS, for the comparison between the species included and those excluded (see
section 1.2.7). Variable names: BM (adult body mass), GT (gestation time), WA
(weaning age), NBM (neonatal body mass), LS (litter size), LY (litters per year), AFB
(age at first birth), RL (reproductive lifespan).

Life history trait	N total	N Excluded	β	T	P	λ
BM	3506	2989	0.06	4.5	<0.001	0.99
GT	1427	909	<0.01	0.1	0.923	0.99
WA	1252	734	<0.01	0.3	0.737	0.92
NBM	1107	589	<0.01	0.2	0.844	0.99
LS	2536	2018	0.03	5.8	<0.001	0.96
LY	1230	712	0.01	1.0	0.307	0.93
AFB	944	426	0.02	1.7	0.096	0.90
RL	748	230	0.09	6.0	<0.001	0.93

2.4 – Alternative transformations for introduction effort

Introduction effort is highly skewed across species since most mammals have been
introduced to one or few locations (main text, section 1.1.2). Following previous
studies (Duncan *et al.* 2001; Forsyth *et al.* 2004; Krivánek *et al.* 2006; van Wilgen &
Richardson 2012), we convert introduction effort into a binary variable with a split at
4, the median number of introduction locations for all introduced species with data on

establishment success (section 1.2.1), for the analysis in the main text and

2   supporting analyses so far presented (sections 2.1, 2.3). Here we show that the main

conclusions of this study remained unaltered once alternative thresholds to convert

4   introduction effort into a binary variable, or the raw data or the log-transformed data,

are used.

6   Consistent with the main analysis (median split at 4 location, main text) we

repeatedly find that, at establishment, litter size and introduction effort are strongly

8   associated with success regardless how introduction effort is analysed (Table S5a).

Likewise, reproductive lifespan has a weaker influence on success at this stage and

10   its effect becomes stronger with a higher threshold for the conversion of introduction

effort into a binary trait (Table S5a). Moreover, no other life history trait is associated

12   with success at this stage in any model (Table S5a).

    At the stage of spread, litter size and introduction effort are strongly associated

14   with success in all models while litters per year has a weaker effect across all models

(Table S5b), as found for the main analysis (main text). No other life history trait is

16   associated with success at this stage with the sole exceptions of marginally older age

at first birth in successful mammals in the model with introduction effort split at 6

18   locations and an older weaning age for successful mammals with introduction effort

split at 3 locations (Table S5b). However, both results are not robust and are not

20   associated with success in any other model regardless of how introduction effort is

analysed (Table S5b). In addition, we note that a small number of species fall in the

22   category 'unsuccessful' (n=13 out of 74 species at this stage) when introduction effort

is split at 3 at this invasion stage (Table S5b).

1 **Table S5.** Phylogenetic GLMM models of success at establishment (a) and spread (b) against all life history traits and introduction effort when introduction
2 effort (IE) is analysed as raw data, log-transformed data or is transformed into a binary variable using different thresholds (establishment stage: n=149;
3 spread stage: n=74; see Figure 1a in the main text). The column labeled 'Transform' indicates how IE is treated and the next column how many species falls
4 in the category '0' for IE treated as binary (N [0]). The median split at 4 is used in the main analysis (0 as ≤4, 1 as ≥5). The remaining columns report the
5 mean *beta* estimates and proportion of overlap with 0 for each variable in the model (section 1.2.3). Variable names: BM (adult body mass), GT (gestation
6 time), WA (weaning age), NBM (neonatal body mass), LS (litter size), LY (litters per year), AFB (age at first birth), RL (reproductive lifespan).

(a) Establishment		IE		BM		GT		WA		NBM		LS		LY		AFB		RL	
Transform	N [0]	β	%	β	%	β	%	β	%	β	%	β	%	β	%	β	%	β	%
Raw data	NA	0.34	0.0	-0.40	32.0	-1.91	21.0	0.57	33.9	0.08	47.2	5.27	2.2	1.31	28.7	0.07	48.4	3.32	6.2
Log$_{10}$	NA	3.61	0.0	-0.39	32.1	-2.22	18.2	0.42	38.5	0.17	43.2	4.45	4.4	1.51	24.8	0.13	46.7	2.71	9.4
≤3, ≥4	64	3.07	0.0	-0.19	40.8	-1.67	23.9	0.89	27.1	0.05	48.4	5.46	1.2	1.36	28.0	0.26	43.7	2.26	12.2
≤4, ≥5	71	2.70	<0.1	-0.30	36.0	-2.20	17.5	0.90	26.0	0.15	42.9	5.51	0.9	1.44	25.9	0.61	34.9	2.49	8.9
≤5, ≥6	81	2.10	<0.1	-0.17	42.0	-1.88	20.6	0.80	28.3	0.05	47.6	5.96	0.7	1.93	17.7	0.39	40.4	2.91	5.2
≤6, ≥7	89	2.43	<0.1	-0.24	37.9	-2.07	18.5	0.76	29.6	0.13	44.3	6.17	0.4	1.84	18.4	0.47	37.1	2.95	5.5
≤7, ≥8	93	2.85	0.0	-0.31	34.2	-1.86	21.5	0.99	23.9	0.08	46.4	5.68	0.7	1.34	26.6	-0.21	44.0	3.20	4.3
≤8, ≥9	96	2.73	<0.1	-0.31	35.1	-1.74	22.6	1.04	22.5	0.05	47.7	5.59	0.6	1.36	25.7	-0.45	37.8	3.27	3.2
≤9, ≥10	101	2.50	<0.1	-0.25	37.3	-1.79	21.1	0.83	27.3	0.06	47.4	5.67	0.5	1.51	22.9	-0.41	38.9	3.33	3.1

7

(b) Spread		IE		BM		GT		WA		NBM		LS		LY		AFB		RL	
Transform	**N [0]**	β	%	β	%	β	%	β	%	β	%	β	%	β	%	β	%	β	%
Raw data	NA	0.04	<0.1	0.61	21.5	0.99	36.8	0.81	33.2	-0.67	25.4	3.56	5.1	2.47	12.9	0.58	35.3	1.09	28.8
Log_{10}	NA	2.14	0.0	0.19	40.1	1.21	36.4	0.91	30.7	-0.61	29.0	3.34	7.2	2.82	12.4	1.23	20.4	0.65	36.6
≤3, ≥4	13	2.82	<0.1	0.16	42.0	-0.77	42.3	2.57	8.9	<0.01	49.8	4.78	2.2	3.71	6.2	1.30	20.6	0.26	44.6
≤4, ≥5	17	1.77	1.0	0.28	36.3	-0.54	43.1	1.96	13.8	-0.23	42.5	3.93	3.7	3.15	8.2	1.55	15.4	0.31	43.1
≤5, ≥6	19	1.85	0.8	0.28	37.0	-0.23	47.3	1.65	18.3	-0.37	37.4	3.86	4.1	3.54	5.5	1.85	11.0	0.76	34.5
≤6, ≥7	25	3.21	0.0	0.34	34.4	0.71	42.0	1.42	23.4	-0.70	27.3	4.40	2.7	3.65	7.5	2.54	5.7	-0.08	47.8
≤7, ≥8	27	3.36	0.0	0.12	43.9	0.12	48.5	2.03	15.9	-0.39	37.1	4.04	4.2	2.82	13.8	1.68	14.5	-0.05	47.7
≤8, ≥9	28	2.90	0.0	0.17	41.3	0.95	38.9	1.52	21.1	-0.57	31.3	3.39	6.5	2.80	13.6	0.92	26.9	0.41	41.9
≤9, ≥10	32	2.23	<0.1	0.30	35.5	0.72	41.7	1.31	23.2	-0.52	32.6	3.75	4.6	3.34	8.6	1.04	25.0	0.82	33.5
≤10, ≥11	34	2.18	<0.1	0.37	31.5	0.37	45.5	1.16	26.0	-0.45	34.5	3.59	4.2	3.54	7.0	0.92	27.4	0.69	35.4

3 – SUPPLEMENTARY DISCUSSION

2 The analyses presented here show that the main conclusion of this study on how life

history traits affect each stage of the invasion pathway are robust. Results do not

4 differ qualitatively once possible issues with multicollinearity among predictors are

considered (section 2.1). Furthermore, our results and conclusions are unlikely to be

6 affected by potential biases associated with the sample of mammals included in our

study (see section 2.3) and by how introduction effort is analysed (section 2.4).

8   Specifically, our conclusions are consistent between full and reduced models after

multicollinearity is considered (section 2.1). The probability of being introduced into

10 novel environments is higher for species with larger and more frequent litters and a

longer reproductive lifespan, as found in the main analysis (sections 2.1). In support

12 of classic theory on how life history traits enable small populations to grow and

escape the risk of extinction due to stochasticity (Pimm 1991), we find that the

14 probability of establishing an alien population is higher for introduced species with

larger litters but, consistent with recent theoretical models (Sæther *et al.* 2004;

16 Jeppsson & Forslund 2012), in conjunction with a weaker contribution of longer

reproductive lifespan (section 2.1). Finally, our finding that established mammals are

18 more likely to spread in non-native regions if they have larger litters and, to a lesser

extent, more frequent litters, is consistent between full and reduced models (section

20 2.1). At spread, we also find a small positive effect on weaning age on the probability

of success when possible issues with multicollinearity are resolved (section 2.1).

22 Success at both the establishment and spread stages increases with greater

introduction effort in the reduced models (section 2.1), as found in the main analysis

24 (main text). Our results also indicate that OV is not an independent life history axis in

mammals (section 2.2).

Sampling biases are unlikely to affect our conclusions (section 2.4). Influential

2   variables in the main analysis that show slight sampling biases are litter size and

reproductive lifespan. However the differences between the species included and

4   excluded in the main analysis are small for such large samples. Finally, the way

introduction effort is treated for the analysis (as raw data, as log-transformed, or as

6   binary with different thresholds; see section 1.1.1) does not influence our conclusions

on which life history traits are influential for success at establishment and spread

8   (section 2.4). Regardless of how introduction effort is analysed, establishment

success is higher for mammals with larger litters and marginally longer lifespan, while

10   success at spread is associated with larger litters and, more weakly, with more

frequent litters. At both stages, greater introduction effort is associated with success.

12   Finally, our approach demonstrates the importance of estimating and accounting

for the phylogenetic signal in the data when testing hypotheses across species on

14   factors promoting success of alien organisms. In all models at all stages of invasion

we find that the strength of the phylogenetic signal is intermediate between 0

16   (species' independence) and 1 (similarity between species is proportional to the time

of common evolution; Freckleton *et al.* 2002). These results indicate that methods

18   assuming that phylogenetic effects are very high (e.g. independent contrasts) or non-

existent (i.e. without phylogeny), are inappropriate and might lead to incorrect

20   conclusions in studies of biological invasions that underestimate or overestimate the

strength of phylogenetic signal. It should be noted that statistical models that include

22   phylogenies evaluate the strength of the phylogenetic signal on latent variables (e.g.

GLMM in this study; Hadfield 2010; Hadfield & Nakagawa 2010; Hadfield 2012) or

24   model residuals (e.g. PGLS; Freckleton *et al.* 2002; Revell 2010). Therefore, such

estimates of phylogenetic signal are based on all available data in a model (in our

26   case invasion success and all predictors) and cannot be used in a simple fashion for

inferring whether closely related species are more or less likely to succeed at

2 different stages than less closely related species.

Altogether this study supports classic theory (Pimm 1991) regarding the role of life

4 history traits in sustaining population growth and demonstrates that along the

invasion pathway barriers at each stage select for species with progressively greater

6 reproductive output; invasive mammals are therefore very fecund.

Our approach of studying invasion at the species level is particularly suited for

8 testing hypotheses on which species traits, as opposed to the location or community

characteristics, promote success of alien organisms (see Section 1.1.2), while also

10 effectively accounting for phylogenetic effects across species. We also demonstrate

that the number of unique introduction locations can be used as a robust and reliable

12 estimate of the magnitude of introduction effort in comparative studies across species

(Sections 1.1.3 and 2.4). We thus argue that the combination of a species level

14 approach like ours, our detailed protocol for the classification of success at each

stage along the invasion pathway from introduction to spread, and the number of

16 introduction locations as an estimate of introduction effort, will be particularly valuable

to investigate which species traits promote invasion success in taxa where detailed

18 data on the number of introduced individuals is unknown or is available for too few

introductions.

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