A Change in response to Cg

B Change in response to Cr

Fig. 3. Change in mobbing response (mandible snaps and rasp calls) of focal birds (one nest per horizontal line) from their baseline (black dot) until after they observed their neighbors (black X) mobbing either (**A**) gray cuckoo morph, Cg, or (**B**) rufous cuckoo morph, Cr. These data are only pairs' responses to the same cuckoo morph they observed their neighbor mobbing ($n = 26$ each). Our measure of mobbing was conservative; any mobbing response < 20 (vertical dashed line) was treated as no response (6).

investment (22) explained the variation in response to social information (table S2). Neither did variation in neighbor attributes such as age, clutch size, or nesting stage explain differences in focal response (table S2). When we considered only focal birds where we were certain whether they had observed their neighbor mobbing, there was also no relationship between attendance at the neighbor's nest and how likely they were to mob cuckoos back at their own nest (29 attended versus 8 not attended; generalized LMM, effect size = 0.43 ± 0.90, $P_{MCMC} = 0.67$).

Although we cannot yet explain it, this variation in the host's response to social information has important consequences. Social learning can be effective as long as there are sufficient demonstrators, which allows a population to change rapidly as information spreads. But spatial heterogeneity in host propensity to respond or learn, and in the local frequency of cuckoos and sparrowhawks, will all influence host and cuckoo success. Recently, spatial heterogeneity of targets and searchers has been shown to influence selection (23) and to facilitate the evolution of polymorphisms (24, 25). However, the possible ways in which information might spread among searchers remains unexplored, as does its role in the evolution of polymorphisms and mimetic defenses. Our results show that the success of both cuckoo morphs will depend not only on their relative frequency, but also on the hosts' information landscape (26).

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Unraveling the Life History of Successful Invaders

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Despite considerable current interest in biological invasions, the common life-history characteristics of successful invaders remain elusive. The widely held hypothesis that successful invaders have high reproductive rates has received little empirical support; however, alternative possibilities are seldom considered. Combining a global comparative analysis of avian introductions (>2700 events) with demographic models and phylogenetic comparative methods, we show that although rapid population growth may be advantageous during invasions under certain circumstances, more generally successful invaders are characterized by life-history strategies in which they give priority to future rather than current reproduction. High future breeding expectations reduce the costs of reproductive failure under uncertain conditions and increase opportunities to explore the environment and respond to novel ecological pressures.

Concern over the impact of invasive species on biodiversity and ecosystem functioning has generated interest in understanding what makes a successful invader (*1*). Although there is evidence that species differ in their invasion potential, controversy exists regarding the features that differentiate successful and un-

successful invaders (*2–4*). Life history—defined as the way organisms allocate time and energy to reproduction, growth and survival (*5, 6*)—has long been at the core of the controversy. It is generally agreed that extinction of introduced populations may result from either demographic stochasticity associated with small population

size or negative population growth due to failure to respond to novel environmental pressures (*2*). Yet how life-history characteristics affect these extinction risks is less clear. Classical theory predicts that prioritizing the reproductive effort confers advantages during invasions by allowing the population to grow faster and hence to reduce the period that it will be threatened by demographic stochasticity (*7*, *8*). Nevertheless, prioritizing future over current reproduction may also confer benefits through a long life span and iterated reproduction, which make the introduced population less vulnerable to stochastic fluctuations and better able to cope with the difficulties posed by the novel environment (*9–12*). Despite being rooted in robust theoretical arguments, confidence in each hypothesis is undermined by a perceived lack of empirical support (*3*, *4*).

To elucidate the importance of life histories on invasion success, we tested these two hypotheses with a global comparative analysis of past avian introductions. Birds are particularly suited for such analyses because accurate information is available for many introduction events, and life-history variation is well documented (*13*). We assembled information on 2760 introduction events, comprising 428 species from 49 families,

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47% of which were successful. The probability of establishment was modeled as a function of the species life-history traits (*14*) with a generalized linear mixed-model (GLMM) framework, which controls for the nonrandom distribution of species across locations and nonindependence resulting from species being introduced to several locations and locations being subject to several introductions (*15*). Results were further supported with demographic models and species-level phylogenetic least-squares models (PGLS).

Our analyses yield little empirical support for the population growth hypothesis. Of the traits previously used as surrogates of population growth, only clutch size is associated with establishment success, when one controls for both taxonomic and regional effects (table S1). Contrary to the hypothesis, however, species that lay larger clutches are worse (not better) invaders (GLMM: $P = 0.002$) (Fig. 1A). We also tested for a direct relation between establishment success and maximum population growth rate (R_{max}), estimated by solving Cole's equation (*16*) and with demographic models (*15*). We found no significant association (GLMM: $P > 0.113$ in all cases) (table S1), which similarly failed to support the hypothesis. The likelihood of establishment increases with the number of individuals introduced (*17*), yet adding propagule size into the model does not change any of the above conclusions (table S1).

The failure to find any effect of population growth on establishment success may reflect two shortcomings of the theory. The first is the assumption that demographic stochasticity is a major cause of extinction of introduced populations. Models and empirical analyses indicate that

the curve relating propagule size to establishment success typically has a threshold above which releasing more individuals does not substantially increase establishment success (*16*). In birds, the estimated threshold is over 300 individuals (Fig. 2A), which implies that >20% of introductions may be beyond the influence of stochasticity. As we restrict the analyses to those introductions that involve a lower propagule size, the effect of R_{max} on establishment success increases (Fig. 2B). Even when the effect continues to be nonsignificant in all cases, this pattern suggests that growing fast is most relevant when propagule size is extremely small (*18*). A simple stochastic demographic model illustrates this point (*15*). On the basis of simulated trajectories during 100 years for 5000 introduced populations, we estimated the probability of establishment as a function of the initial propagule size for different population growth rates. The simulations reveal that high population growth rates allow the invader to avoid demographic stochasticity (Fig. 2C), as predicted by theory (*19*), but the effect is only noticeable when the number of individuals released is remarkably low (*18*).

The second shortcoming of the hypothesis is that it ignores that a high reproductive effort entails costs in terms of reduced survival. The resulting trade off defines a "fast-slow" axis of life-history variation from "highly reproductive species" (fast-lived) at one end to "survivor species" (slow-lived) at the other end (*20*). Although a fast-lived species can recover more rapidly from a small population size (fig. S1B), demographic models show that this advantage may be in part countered by an increased risk of extinction through population fluctuations resulting from

Fig. 1. (**A** to **F**) Species invasion potential as a function of life-history traits. The invasion potential is the random effect coefficients obtained from a GLMM controlling for taxonomy, country, and introduction effort. The *P* values come from a PGLS that validates the effect of each variable on the invasion potential.
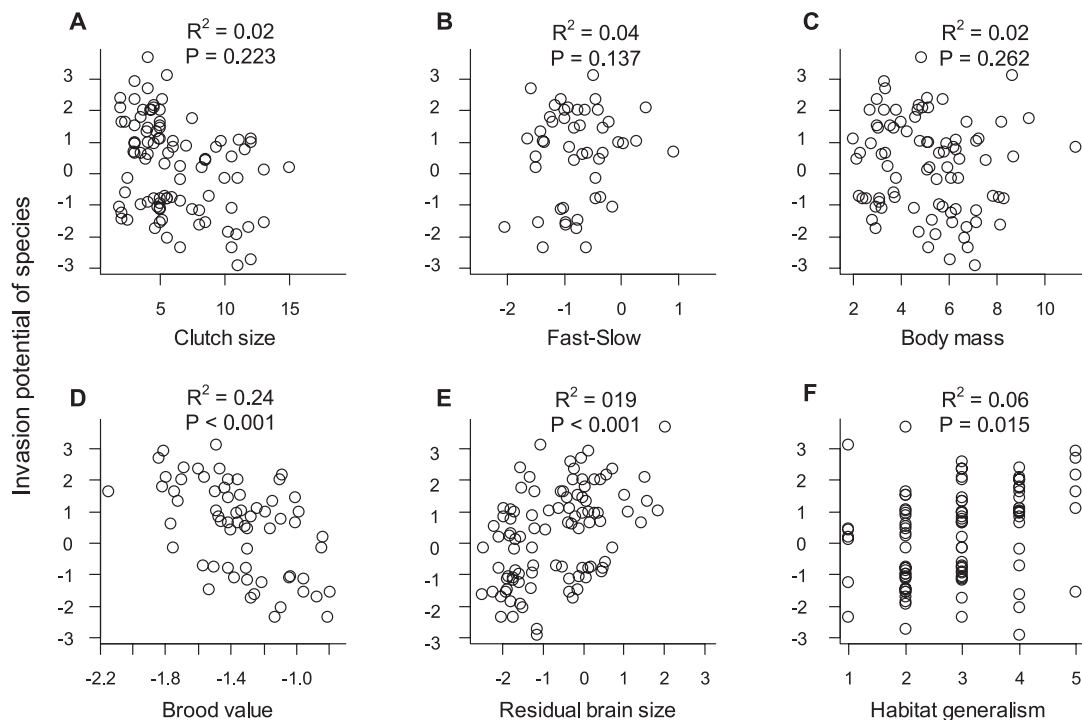
Fig. 2. (**A**) Relation between establishment success and propagule size based on historical introductions. (Inset) Zoom on the interval of lowest propagule size. The curve has been fitted with the function "nls" from the "MASS" R package. (**B**) Effect size (± standard error) of the relation between establishment success and population growth rate when the analysis is restricted to introductions of, respectively, <5, 10, 25, 50, 100, and 300 individuals and when considering all introductions. (**C**) Probabilities of establishment as a function of propagule size for different finite population growth rates (lambdas), derived from 5000 populations simulated over 100 years with a stochastic demographic model. (**D**) Probabilities of establishment derived from the same model as a function of the fast-slow continuum.
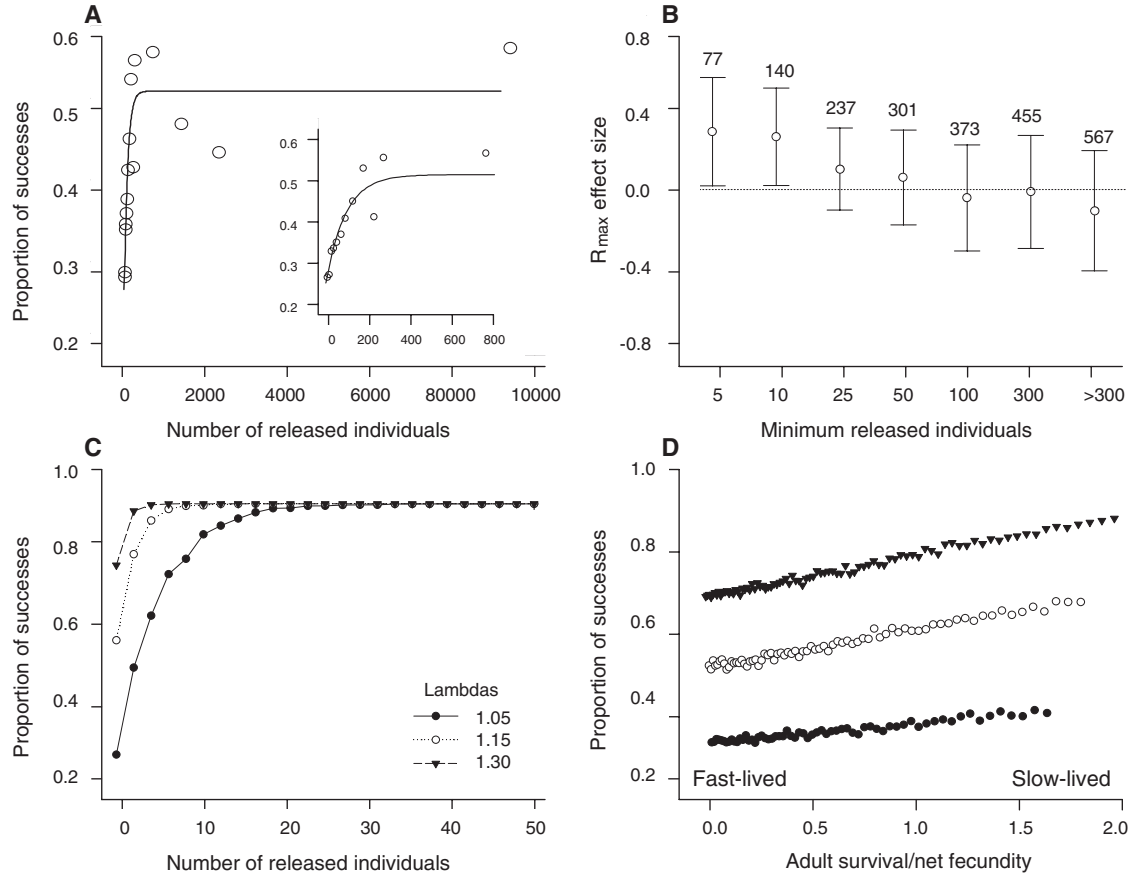
demographic stochasticity (Fig. 2D) (*11*). A critical issue is therefore whether introduced species can maintain high reproductive rates in environments to which they have had little opportunity to adapt. Theory predicts that fast-lived species should generally experience greater difficulties in novel environments than slow-lived ones, as they are less likely to have adaptations that buffer individuals from extrinsic factors (*8, 21*). Body size and brain volume have been suggested to be such adaptations (*2, 13*). Although our analyses yield little general support for body size, they confirm previous findings that a large brain relative to body size promotes establishment (Fig. 1, C and E; Table 1; and table S2) (*22*). A large brain is thought to assist animals in novel environments by enhancing their ability to construct behavioral responses to novel ecological challenges (*23*). When relative brain size is included in the models, the fast-slow continuum approaches significance in the direction predicted by the population growth hypothesis (GLMM: $P = 0.065$), and the effect of clutch size on establishment success becomes nonsignificant ($P = 0.177$) (table S1).

Our results do not invalidate the "population growth" hypothesis but suggest that growing fast will only be advantageous in very special cases, when the founder population is small and when the ecological pressures posed by the new en-

vironment are moderate (e.g., when there is environmental matching between the regions of origin and introduction). It is nonetheless possible that reproductive effort exerts greater influence on establishment success in organisms with more limited capacity than birds to explore the environment and to develop behavioral responses to novel challenges.

As an alternative to the population growth hypothesis, we ask whether successful invaders are better characterized by life-history strategies that prioritize future over current reproduction. Such a strategy relies on distributing reproductive effort across a number of events. This may have

two major consequences under the uncertainties of a novel environment. First, it reduces the fitness costs of a reproductive failure by spreading the risk over several reproductive events (*10*). Second, it allows delaying or skipping reproduction and engaging in reproductive activities only when conditions are favorable (*9, 24*). These consequences are not well described by the fast-slow continuum, as even relatively short-lived species may reduce the cost of losing a clutch by reproducing several times in the same season. A more general metric is provided by the brood value concept (*25*), which is expressed as $\log_{10}\{1/[(\text{broods per year}) \times (\text{reproductive}$

Table 1. Fixed-effect and random-effect parameters in the best-ranked model accounting for variation in establishment success. The model is based on 635 introductions and is the result of an automated model selection procedure including all combinations of life-history traits and confounding variables. SE, standard error; SD, standard deviation

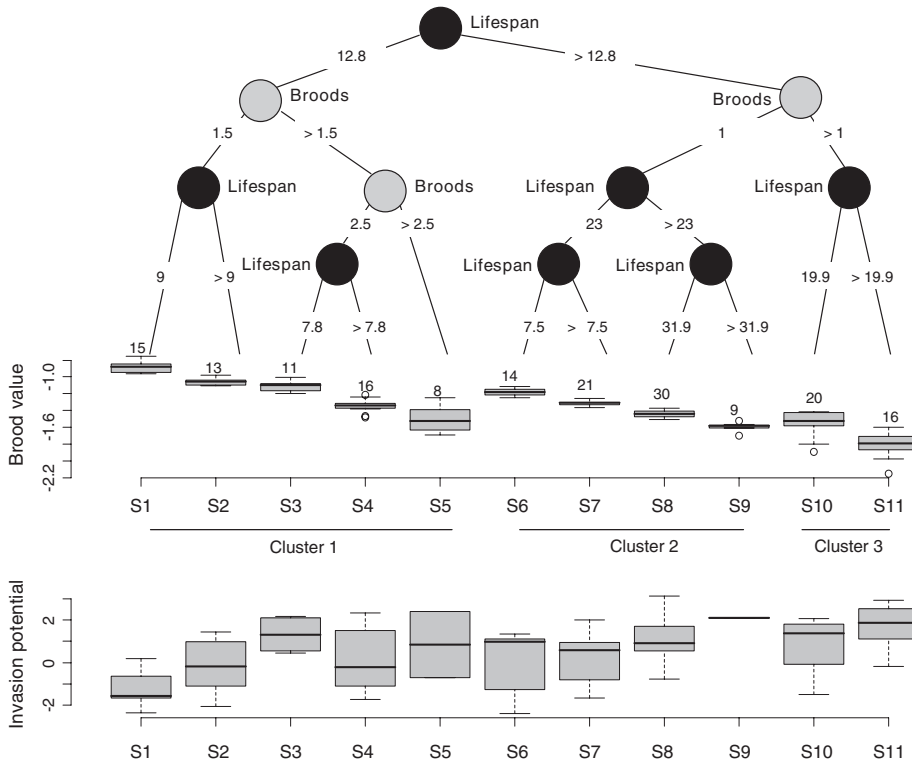| Fixed effects	Estimate	SE	z	P
Brood value	−2.078	0.771	−2.69	0.0071
Propagule size	0.452	0.062	7.28	<0.0001
Relative brain size	0.535	0.204	2.62	0.0092
Habitat generalism	0.750	0.199	3.77	<0.0001
Random effects	Variance	SD	Likelihood ratio test	P
Species	1.784	1.335	39.69	<0.0001
Country	2.989	1.729	34.83	<0.0001

Fig. 3. Tree regression describing brood value as a function of the number of broods per year (gray dots) and maximum life span (in years, black dots). The graphs in the bottom show the median and percentiles of the brood value and invasion potential for each strategy (from S1 to S11). Differences in brood value between strategies are all significant at $P < 0.05$ except for the pairs S4-S7, S5-S10, and S9-S10.

life span)]}. A high brood value means that all reproductive effort is allocated into a few reproductive events and, hence, that each brood has high fitness value, whereas a low brood value means that the effort is distributed into many attempts, whether in a same season or in different ones. Variation in brood value is poorly correlated with the fast-slow continuum and R_{max} (fig. S1, C and D), which shows that it represents a somewhat different life-history axis (figs. S2 and S4).

As predicted, species with low brood values show a higher probability of establishment than those with a high brood value (GLMM: -2.313 ± 0.520, $z = -4.44$, $P < 0.0001$, $n = 1943$ introduction events) (Fig. 1D). The association holds when removing outliers ($P < 0.0001$) and when considering other factors that may also enhance establishment, such as high propagule size, large brains, climate matching, habitat generalism, and introduction on an island (Table 1 and tables S2 and S3). However, there is no single strategy to be a successful invader (Fig. 3). Indeed, either species that combine several broods per year with a relatively short life span or those that lay a single clutch per year but have a very long life span are significantly more successful than species with high brood values (table S4). This may explain why phylogenetically closely related species often exhibit striking differences in invasion potential (fig. S6).

The observation that a strategy based on future reproductive returns facilitates invasion success integrates a variety of theories, including bet-hedging (*10*), life history–buffering (*11*, *26*) and cognitive-buffer (*23*) theories, which conceptualize life histories as evolutionary solutions to environmental uncertainties. For an invader, unfamiliarity and insufficient adaptation to resources, enemies, and other hazards are likely to increase the risk of reproductive failure (*27*). Consequently, the inability to spread the risk over several breeding attempts and/or to delay reproduction if conditions are unfavorable may have important costs. By adopting a future-returns strategy, however, individuals not only reduce these costs but also increase the opportunities for acquiring environmental information and, through behavioral adjustments, improve performance on exploiting the resources and avoiding the enemies.

Our results yield firm evidence for the long-standing, yet poorly supported, suggestion that life history does influence invasion success. However, the mechanisms seem to be complex and different from those generally considered in the invasion literature, which may explain the past difficulties in disentangling the life history of successful invaders. Although our results do not preclude that a high reproductive effort may offer advantages during the invasion process, they highlight that, in terms of being a successful invader, it can pay to have life-history strategies that increase the value of adults over the value of offspring even at the cost of reduced reproduction.

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15. Materials and methods are available as supplementary materials on *Science* Online.
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Supplementary Materials
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Figs. S1 to S8
Tables S1 to S4
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