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Heterosis, the catapult effect and establishment success of a colonizing bird

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The genetic basis of population colonization is poorly understood, particularly in animals. Here, I introduce the idea of a 'catapult effect' to explain how the effects of transient increases in fitness can be retained in population demography diminishing the chance of extinction. I tested this idea using information on historical introductions of hybrid and non-hybrid pheasants in the United States. I found that hybrid pheasants were 2.2 times more likely to establish than non-hybrid strains. Analysis of fitness components failed to support the alternative that the increased odds of establishment resulted from increased genetic variation conferring permanent fitness benefits through directional selection or by purging deleterious alleles. These results show that even ephemeral increases in fitness can affect the persistence of small populations.

Keywords: biological invasion; establishment; extinction; heterosis; hybrid vigour; *Phasianus colchicus*

1. INTRODUCTION

Colonization is a key ecological process involved in maintaining species diversity and population persistence (Hubbell 2001; Lande *et al.* 2003) while colonization by invasive species obstructs conservation, threatens native species and imposes a significant economic burden (Mooney & Hobbs 2000). In animals, colonization success is related to numerous aspects of ecology including propagule pressure (Lockwood *et al.* 2005), escape from natural enemies (Torchin *et al.* 2003; Colautti *et al.* 2004), and niche breadth (Vazquez 2006). However, the genetic basis of colonization success is only beginning to be unravelled. In particular, while heterosis ('hybrid vigour') has been shown to increase invasiveness in plants (Ellstrand & Shierenbeck 2000; Moody & Les 2002), in sexually reproducing species heterosis erodes rapidly due to segregation and does not confer permanent fitness benefits (Lee 2002). Hence, conventional theory would predict that heterosis does not affect establishment success. Using data from introductions of ring-necked pheasants (*Phasianus colchicus*) in the United States, I tested the idea that heterosis contributes to establishment success in sexually reproducing species via a 'catapult effect', where introduced populations establish an incipient toehold during the F_1 generation. I estimated that the odds of successful establishment for hybrid pheasants is 2.2 times greater than for parent sub-species and that this is probably a result of heterosis rather than of selection on increased genetic variation resulting from hybridization. These results underscore that the interaction between ecological and genetic factors is crucial for understanding colonization processes.

It is well known that fitness advantages during the early stages of exponential population growth reduce the chance of immediate extinction (MacArthur & Wilson 1967; Carson 1975; Renshaw 1991), though the prevalence and causes of fitness differences during colonization are poorly studied, particularly in animals (Williamson 1996; Lee 2002). Although heterosis has been detected in descendents of naturally immigrating song sparrows (*Melospiza melodia*; Marr *et al.* 2002) and introduced greater prairie chickens (*Tympanuchus cupido pinnatus*; Westemeier *et al.* 1998) and hybridization has been shown to increase the advance of an invasive crayfish (*Orconectes rusticus*; Perry *et al.* 2001), heterosis has not been shown to increase establishment success in introduced animals. There are two mechanisms by which hybridization could increase establishment success in sexually reproducing species. First, hybridization could result in permanent changes to the genetic composition of the population by increasing genetic variance on which selection could operate or by eliminating deleterious recessive alleles (Lee 2002). This is not a heterotic effect. Second, heterosis might increase fitness in the F_1 generation, projecting the population from small size with high chance of extinction through demographic stochasticity to large size buffered against such extinction risk, a phenomenon that might be referred to as a 'catapult effect'. Figure 1 illustrates this idea graphically; a quantitative model with numerical examples is presented in text 1 of the electronic supplementary material. Empirically, these two situations are distinguished by the transience of the fitness difference due to hybridization.

2. MATERIAL AND METHODS

(a) *Data*

I compiled records of 628 introductions of ring-necked pheasants in the United States between 1960 and 1978 including information about the success or failure of the population to establish, propagule pressure and whether survival or reproduction was observed after release (table 1 of electronic supplementary material). A measure of annual propagule pressure was obtained for each introduction record by dividing the total number of individuals introduced by the number of years over which introductions occurred (usually, but not always, 1) and transforming to a log scale. Propagule pressure (the logarithm of the number of individuals introduced) was included as a covariate because it is a well-known correlate of introduction success (Lockwood *et al.* 2005) and has confounded interpretation of previous analyses (Cassey *et al.* 2004*a*). Dependent variables (generally qualitative observations) were scored as: (i) evidence of survival (binary response), (ii) evidence of reproduction (binary response) and (iii) evidence of establishment (ordered response: 0, 'failed'; 1, 'probably failed'; 2, 'probably established'; 3, 'established'; see text 2 of electronic supplementary material for details). As there was strong evidence of establishment (response = 3) for only seven populations, records were grouped, resulting in 179 introductions that 'failed' or 'probably failed' and 128 introductions that 'established' or 'probably established'.

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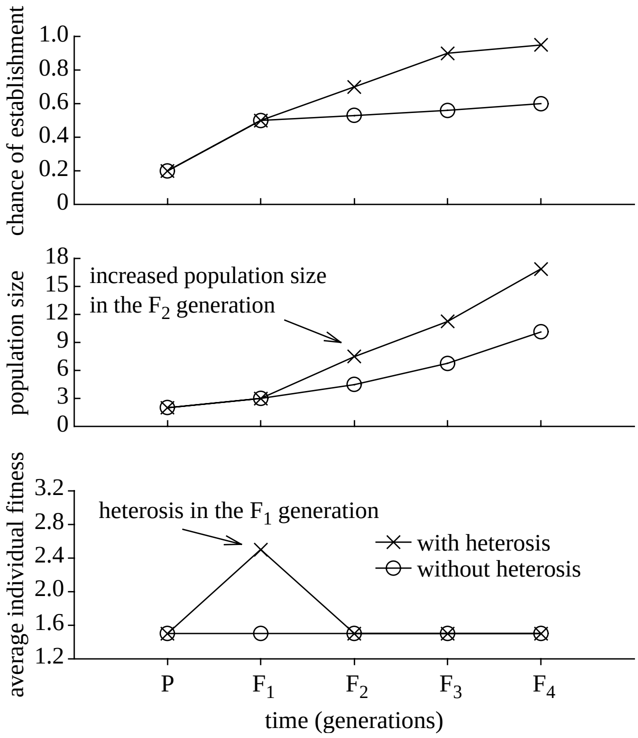

Figure 1. Graphical model of the catapult effect, a hypothesized mechanism by which heterosis in sexually reproducing populations could increase establishment success. Although fitness increases from heterosis in sexually reproducing species will be transient, the catapult effect supposes that the differential fitness conferred by heterosis might be maintained via demographic memory. The idea is illustrated by tracking at each generation in the introduced population: (i) average individual fitness, (ii) population size and (iii) conditional chance of establishment. Compare the trajectories for a population exhibiting heterosis (crosses) with a population not exhibiting heterosis (circles). In the F_1 generation, the population exhibiting heterosis shows an increase in average individual fitness. In populations of small size, the increase in fitness in the F_1 generation of the heterotic population results in an increase in the population size in the F_2 generation, relative to the non-heterotic population. Generally, the chance of long-term persistence is a monotonic increasing function of population size. Thus, defining the chance of establishment as the complement of the chance of extinction conditioned on the size of the F_2 generation, the chance of establishment for the heterotic population is greater than the chance of establishment for the non-heterotic population. Because of sexual reproduction, average individual fitness in the heterotic population returns to the level of the parent generation by the F_2 generation. However, as long as the relative difference in population size obtained in the F_2 generation is maintained, the average conditional chance of extinction will generally be greater in the non-heterotic population (see text I of electronic supplementary material).

(b) *Statistical analysis*

To test for effects of parent strain, hybridicity and propagule pressure, I fit the generalized linear model with binomial distribution and logit link function (logistic regression) with mean

$$\eta = \beta_0 + \beta_1 x_{\text{bianchii}} + \beta_2 x_{\text{karpowi}} + \beta_3 x_{\text{persicus}} + \beta_4 x_{\text{robustipes}} + \beta_5 x_{\text{talischensis}} + \beta_6 x_{\text{torquatus}} + \beta_7 x_{\text{hybrid}} + \log(x_{\text{propagules}}), \quad (2.1)$$

where x_{bianchii}, x_{karpowi}, x_{persicus}, $x_{\text{robustipes}}$, $x_{\text{talischensis}}$ and $x_{\text{torquatus}}$, are the number of parents of each sub-species, x_{hybrid} is an indicator variable of hybrid introductions and $x_{\text{propagule}}$ is the average number of individuals introduced per year. Because each introduction comprises two parent sub-species, in the absence of effects of hybridicity and propagule pressure, the response is an average of the two parental lines. Thus, consistent with the definition of heterosis (e.g. Lee 2002), any effect of hybridicity is represented as additive to the average effect of the parents. Since none of the coefficients β_1 through β_6 was significant, meaning that there was no detectable difference between sub-species, I fit the reduced model with mean

$$\eta = \beta_0 + \beta_7 x_{\text{hybrid}} + \log(x_{\text{propagules}}). \quad (2.2)$$

3. RESULTS AND DISCUSSION

Overall, there was evidence of establishment in 128 of 307 (41.6%) introduced populations (figure 2). Propagule pressure ranged from 3 to 8832 individuals yr^{-1}. The full model (regression equation (2.1)) showed no evidence for a difference between sub-species in establishment success (p-values around 0.98), so a second model was fitted including only the hybrid effect and the effect of propagule pressure (regression equation (2.2)). In this model, the effect of hybridicity was highly significant, ($p=0.001$; odds ratio at the maximum likelihood estimate was 2.21), though propagule pressure was not ($p=0.178$). The coefficient of hybrid status in the model can be interpreted as an estimate of the heterotic effect (see §2), which is defined as an increase in fitness compared to the average of the parent strains after accounting for propagule pressure. These results confirm that hybrid status had a significant effect on the establishment success of introduced ring-necked pheasants in the United States.

The effect of hybridicity can only be interpreted as evidence for the catapult effect if permanent fitness benefits can be excluded. Information about survival and reproduction were available for 56 and 149 introductions, respectively. To test for effects of hybridicity on survival and reproduction, I fitted the logistic regression models described above using evidence of survival or reproduction as dependent variables. No variables were significant predictors of survival in either the full model or the reduced model that excluded effects of parent strains ($\alpha=0.05$). Only propagule pressure had a significant effect on reproduction ($p<0.0001$). An alternative approach to distinguish heterosis from permanent fitness increases is the logistic regression with propagule pressure, hybridicity, survival and reproduction all as independent factors. In this model, no variables were significant, though this model was compromised by relatively few records for which all of these factors were measured ($n=30$). For further details, see text III of electronic supplementary material. A correlation between an index of habitability and preference for introducing hybrids showed no evidence of possible confounding from preferentially releasing hybrids in more suitable environments (Kendall's $\tau=3.98$; $p=0.953$; see text III of electronic supplementary material for details).

The first result reported here establishes that hybrid pheasants were more likely to establish than non-hybrid sub-species. The second result suggests that this effect is probably not due to a permanent increase in fitness or statistical artefacts. Together these results suggest that heterosis can increase establishment success in animals, despite the erosion of heterotic fitness gains by segregation. However, this conclusion should be interpreted cautiously given the unbalanced

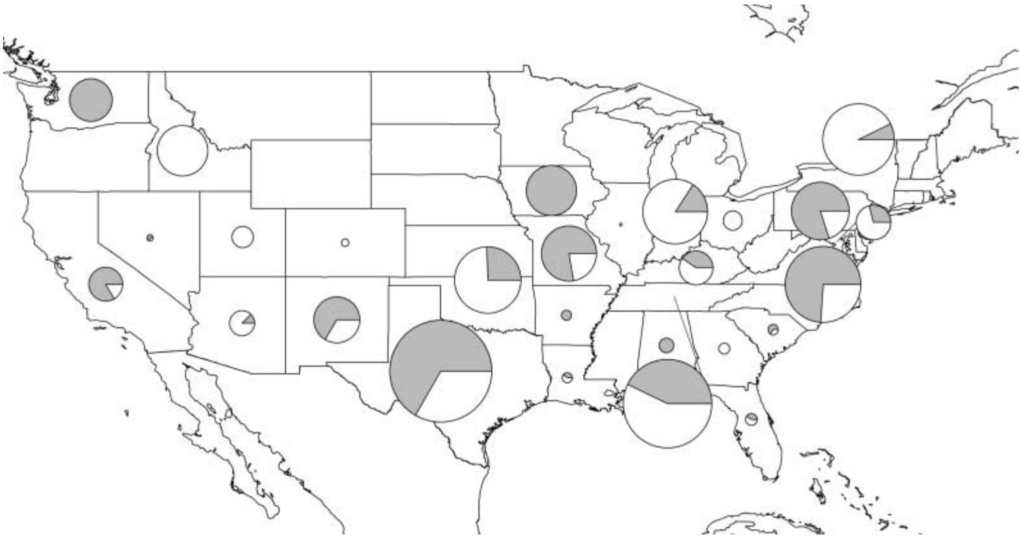

Figure 2. Establishment success of pheasant introductions in the United States. Each pie graph shows the fraction of introductions that resulted or probably resulted in establishment (grey) and the fraction of introductions that failed to result or probably failed to result in establishment (white). The size of the graph indicates the total number of birds introduced in the state during the period 1960–1978, ranging from 77 (Illinois) to 46 259 (Texas).

data used in the analysis. More conclusive evidence could be obtained from a controlled experiment comprising paired releases in which propagule pressure was directly manipulated. Unfortunately, as for many species, the practical and ethical obstacles to experimental introductions are considerable and potentially prohibitive, forcing reliance on data from historical or natural introductions.

The genetic basis of animal invasiveness is an active area of research. Recent findings such as that invasiveness of Argentine ants *Linepithema humile* is associated with decreased genetic variation (Tsutsui *et al.* 2000) and that invasive populations of zebra mussels *Dreissena polymorpha* show higher genetic variation than expected (Stepien *et al.* 2002) are improving our understanding of the biological basis of colonization, although these studies—which draw opposing conclusions for two different groups of animals—illustrate that the genetic basis of invasiveness is not universal. Together with this study, these results underscore that establishment and spread are separate phases of invasion that may have different underlying causes and that invasiveness in general is underdetermined by genetics. Further, the genetic bases of establishment and spread of domesticated and semi-domesticated species like pheasants have probably been affected by long-term cohabitation with humans and, as a result of selection, may exhibit qualitatively different patterns than species that do not occupy modified habitats. Opportunities abound for hybridization between domesticated and non-domesticated animal lineages and between long-isolated strains of many species in modified environments increasingly dominated by human commerce, including trade in organisms (Mooney & Hobbs 2000; Cassey *et al.* 2004*b*). Finally, this finding that temporary increases in fitness from heterosis can increase the chance of population persistence might be incorporated in efforts to safeguard endangered species, particularly when there is the possibility of interbreeding captive and wild animals.

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