

Propagule pressure and persistence in experimental populations

John M. Drake^{1,2,*}, Peter Baggenstos^{1,†} and David M. Lodge¹

¹Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

²National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA

*Author for correspondence (drake@nceas.ucsb.edu)

†Current address: 4100 Saddle Rock, Butte, MT 59701, USA

Average inoculum size and number of introductions are known to have positive effects on population persistence. However, whether these factors affect persistence independently or interact is unknown. We conducted a two-factor experiment in which 112 populations of parthenogenetic *Daphnia magna* were maintained for 41 days to study effects of inoculum size and introduction frequency on: (i) population growth, (ii) population persistence and (iii) time-to-extinction. We found that the interaction of inoculum size and introduction frequency—the immigration rate—affected all three dependent variables, while population growth was additionally affected by introduction frequency. We conclude that for this system the most important aspect of propagule pressure is immigration rate, with relatively minor additional effects of introduction frequency and negligible effects of inoculum size.

Keywords: colonization; *Daphnia magna*; immigration; propagule pressure; renewal process

1. INTRODUCTION

Colonization is a fundamental ecological process. The theory of colonization has been advanced to understand topics as diverse as the biology of dispersal (Clobert *et al.* 2001), persistence of populations (Haccou & Iwasa 1996; Haccou & Vatunin 2003) and metapopulations (Diamond 1975; Hanski 1999), the evolution of life histories (Heino & Hanski 2001; Hanski *et al.* 2002), and the maintenance of genetic (Hartl & Clark 1997) and species (Robinson & Dickerson 1987; Hubbell 2001) diversity. Increasing introductions of non-indigenous species (Carlton & Geller 1993; Ricciardi 2001) and genetically engineered organisms (Kareiva *et al.* 1996) have stimulated research about colonization processes so that risk analyses of anthropogenic introductions may be based on ecological theory (Mack *et al.* 2000). Propagule pressure, the rate a species is introduced into an ecosystem, is a key element explaining why some populations persist while others do not (Forsyth & Duncan 2001; Kolar & Lodge 2001; Cassey *et al.* 2004; Lockwood *et al.* 2005).

Evidence for effects of propagule pressure on population persistence has been compiled from

observational and experimental studies. Recent reviews confirm that successful establishment of insects, zooplankton, fishes, birds and mammals is correlated with the number of organisms introduced (inoculum size) and with the number of introduction events (Veltman *et al.* 1995; Kolar & Lodge 2001; Duncan *et al.* 2003; Cassey *et al.* 2004; Lockwood *et al.* 2005). However, so far only effects of inoculum size have been shown experimentally (Crowell 1973; Ebenhard 1989; Ahlroth *et al.* 2003). Determining the effect of interactions between inoculum size and number of introductions is an important question for research (Lockwood *et al.* 2005). Here, we report results of an experiment in which we used different levels of inoculum size and introduction frequency (number of introductions per unit time) to test for effects on persistence of water fleas (*Daphnia magna*). To our knowledge, this is the first demonstration of the effects of inoculum size and introduction frequency on persistence.

2. METHODS

(a) Experiment

Daphnia are a common model for experimental population dynamics and have been used previously to study persistence (Drake & Lodge 2004; Drake 2005). Our experiment comprised seven replicate populations for two experimental factors (inoculum size and introduction frequency) at four levels each in a blocked arrangement for a total of $7 \times 4^2 = 112$ populations. Experimental microcosms were plastic containers filled with approximately 750 mL of groundwater and inoculated with different numbers of parthenogenetic (female) *D. magna*, depending on treatment. Factors were the number of individuals (2, 4, 6, or 8) added to the population during each introduction event, and the frequency at which introductions occurred (every 2, 4, 6, or 8 days). By using the frequency of introduction as our factor rather than the number of introductions, we can interpret the interaction biologically as the overall rate of immigration (immigration rate = size \times frequency). Thus, our design comprised 11 levels of immigration for many of which there are different combinations of inoculum size and frequency (table 1). Populations were initialized by their first introduction event and were counted daily. Introduced individuals of unknown age and size were haphazardly selected from stock populations and added to persisting populations after counting. No individuals were added to extinct populations. Non-extinct populations were maintained in a greenhouse for 41 days with natural photoperiod (ranging from 9.2 to 10.4 h of light) and ambient temperature *ca* 21 °C. Food was provided *ad libitum* as *Selenastrum* sp. cultured in a dilute solution of Alga-gro medium (Carolina Biological Supply Company).

(b) Hypotheses and statistical analysis

(i) Hypothesis 1: realized population growth rate

Realized population growth rate refers to the difference between final and initial population sizes. We expected the largest effect to be a positive relationship between immigration rate and final population size.

Table 1. Immigration rate (number per day) is the product of introduction frequency and the number of *Daphnia* introduced per event in a laboratory experiment.

introduction frequency	number of <i>Daphnia</i> introduced per event			
	<i>N</i> =2	<i>N</i> =4	<i>N</i> =6	<i>N</i> =8
<i>Daphnia</i> addition every 8 days	0.25	0.50	0.75	1
<i>Daphnia</i> addition every 6 days	0.33	0.67	1	1.33
<i>Daphnia</i> addition every 4 days	0.50	1	1.50	2
<i>Daphnia</i> addition every 2 days	1	2	3	4

However, inoculum size and introduction frequency might also affect final population size through their effect on demographic variance. We reasoned that after controlling for immigration rate, inoculum size would be negatively associated with population growth rate and introduction frequency would be positively associated with population growth rate as combinations of low frequency and large inoculum size would result in larger variance compared to combinations of high frequency and small population size for a given introduction rate. For example, two different ways of obtaining the immigration rate of one individual per day are to introduce one individual every day or two individuals every two days. The second case (larger inoculum size introduced less frequently) would result in a higher demographic variance, which might reduce realized population growth rate. Thus, we hypothesized that population growth rate would be positively related to immigration rate and introduction frequency and negatively related to inoculum size. We tested these hypotheses with multiple linear regression.

(ii) *Hypothesis 2: persistence*

We scored persistence according to whether or not each population was extant at the end of the experiment. Reasoning that immigration rate (the product of inoculum size and introduction frequency) is the most parsimonious explanation of persistence, we first tested for its effect with Kendall's τ for non-parametric correlation, providing a conservative test of our hypothesis. Obtaining a significant result, we performed logistic regression to estimate any additional effects of inoculum size or introduction frequency.

(iii) *Hypothesis 3: time-to-extinction*

Time-to-extinction is predicted to decrease with demographic variance. Reasoning as above, we predicted that for a given immigration rate combinations of low frequency and large inoculum size would result in larger demographic variance reducing time-to-extinction. We tested for effects of experimental factors on time-to-extinction with Cox proportional hazards regression for right-censored observations (Cox & Oakes 1984).

3. RESULTS

(a) *Hypothesis 1: realized population growth rate*

Population size on the final day of the experiment (day 41) increased with introduction frequency and

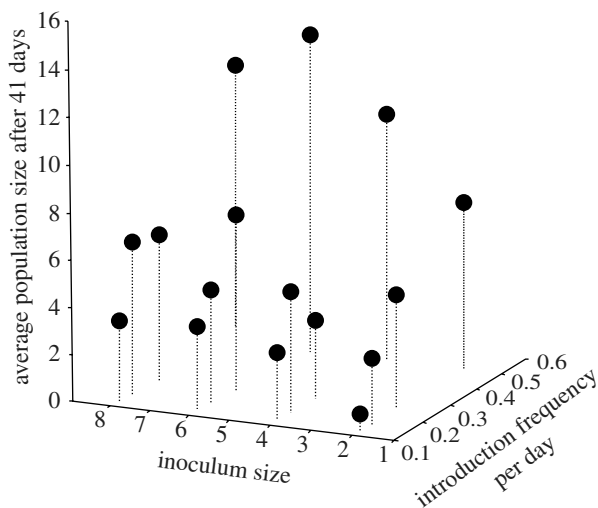


Figure 1. Average population size in experimental populations after 41 days increases with immigration frequency and inoculum size.

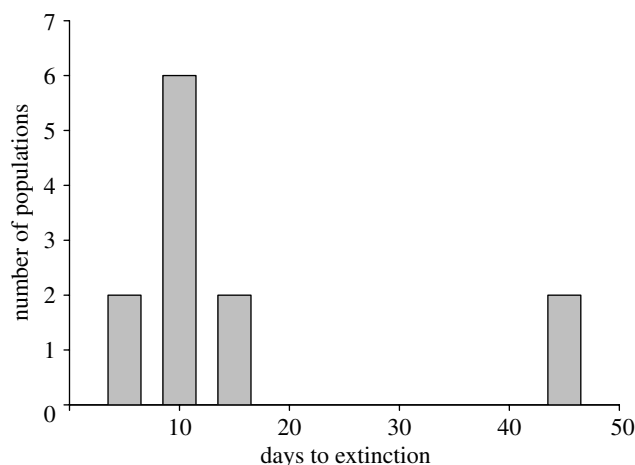


Figure 2. The distribution of observed extinction times ($N=12$) in experimental populations.

inoculum size (figure 1). Not surprisingly, immigration rate had a significant effect on final population size ($p < 0.0001$; $R^2_{\text{fullmodel}} = 0.46$). Introduction frequency also had a significant positive effect on final population size ($p = 0.007$), while there was no detectable effect of inoculum size ($p = 0.928$).

(b) *Hypothesis 2: persistence*

Of 112 total populations, 12 (10.7%) went extinct during the 41 day duration of the experiment. For all populations that went extinct, the mean time to extinction was 13.2 days (s.d. = 13.3 days; figure 2).

Table 2. Models of inoculum size and introduction frequency were fit to extinction time data from experimental populations. (Statistical significance of tests for experimental effects on time-to-extinction were computed with Cox proportional hazards regression. Negative log-likelihood scores indicate that the data marginally support model 1 compared with models 2–5.)

	experimental factor			negative log-likelihood
	inoculum size	introduction frequency	immigration rate	
model 1	$p=0.23$	$p=0.17$	$p=0.61$	42.97
model 2	$p=0.51$	n/a	$p=0.045$	44.18
model 3	n/a	$p=0.28$	$p=0.055$	43.57
model 4	$p=0.032$	$p=0.035$	n/a	43.09
model 5	n/a	n/a	$p=0.0085$	44.40

Consistent with our prediction, immigration rate was positively correlated with persistence (Kendall's $\tau=0.28$, $p<0.0001$). As expected, immigration rate had a significant positive effect on persistence in logistic regression ($p=0.009$). Neither inoculum size nor introduction frequency was significant when included as covariates, either separately or in a single model ($\alpha=0.05$).

(c) Hypothesis 3: time-to-extinction

Minimum and maximum times-to-extinction were 5 days and 41 days, respectively. We fit Cox regressions to all five possible combinations of the two experimental factors (table 2). Coefficients were never significant for anything other than immigration rate in models with both immigration and one or both of inoculum size and introduction frequency, providing no evidence that inoculum size or introduction frequency contributed to time-to-extinction beyond their contribution to introduction rate (table 2: models 1, 2 and 3). The remaining two models represent additive (model 4: inoculum size + introduction frequency) and multiplicative (model 5: immigration rate = inoculum size \times introduction frequency) effects of experimental factors, respectively. The negative log-likelihood scores for these models differ only by 1.3, suggesting that there is no difference between the additive and multiplicative models. Indeed, the maximum difference among all models was only 1.4.

4. DISCUSSION

Theories in conservation biology (Diamond 1975), metapopulation ecology (Hanski 1999), population ecology (Haccou & Iwasa 1996; Matis & Kiffe 2000; Haccou & Vatunin 2003) and invasion biology (Leung *et al.* 2004; MacIsaac *et al.* 2004) have emphasized the importance of immigration for population persistence. Though the contribution of immigration to population growth rate is typically small, immigration is of considerable importance in stochastic models (Bailey 1964; Renshaw 1991; Matis & Kiffe 2000), and in nature, where rescue effects dramatically enhance growth of nearly extinct populations (Brown & Kodric-Brown 1977; Gotelli 1991).

We have shown that for a model system immigration rate was positively associated with persistence, final population size, and time-to-extinction, consistent with theory (Haccou & Iwasa 1996; Haccou &

Vatunin 2003). Further, in our experiment about half of the variation in final population size was explained by experimental factors associated with immigration ($R^2=0.46$), leaving demographic stochasticity and residual uncontrolled variation to account for the remainder. The fact that immigration accounted for such a large fraction of the overall variation in observed population sizes underscores its importance for population persistence and growth in small populations; in this case, immigration was at least as important as demographic stochasticity, which is far more commonly studied.

How the components of propagule pressure— in inoculum size and introduction frequency— affect persistence in assemblages of multiple species is currently unknown, though there is a body of research on the effect of introduction rate on species richness (e.g. Robinson & Dickerson 1987; Robinson & Edgemon 1988). We speculate that introduction frequency will be crucial to persistence of populations with low average individual fitness resulting from inter-specific interactions, particularly in competitively structured communities that, if unperturbed, eventually result in exclusion. As initial colonization and persistence of introduced propagules in such communities is affected by environmental fluctuations (Davis *et al.* 2000), the interaction of environmental variation and immigration rates on different time scales is an important topic for research.

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- Ahloth, P. *et al.* 2003 Founder population size and number of source populations enhance colonization success in waterstriders. *Oecologia* **137**, 617–620.
- Bailey, N. T. J. 1964 *The elements of stochastic processes*. Wiley series in probability and mathematical statistics. New York: Wiley.
- Brown, J. H. & Kodric-Brown, A. 1977 Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* **58**, 445–449.
- Carlton, J. T. & Geller, J. B. 1993 Ecological roulette: the global transport of nonindigenous marine organisms. *Science* **261**, 78–82.

- Cassey, P., Blackburn, T. M., Sol, D., Duncan, R. P. & Lockwood, J. L. 2004 Global patterns of introduction effort and establishment success in birds. *Proc. R. Soc. B* **271**(Suppl. 6), S405–S408. (doi:10.1098/rsbl.2004.0199)
- Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D. 2001 *Dispersal*. Oxford, UK: Oxford University Press.
- Cox, D. R. & Oakes, D. 1984 *Analysis of survival data* Oxford Series in Ecology and Evolution, vol. 21. London: Chapman & Hall.
- Crowell, K. L. 1973 Experimental zoogeography: introductions of mice to small islands. *Am. Nat.* **107**, 535–558.
- Davis, M. A., Grime, J. P. & Thompson, K. 2000 Fluctuating resources in plant communities: a general theory of invisibility. *J. Ecol.* **88**, 528–534.
- Diamond, J. M. 1975 The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biol. Conserv.* **7**, 129–146.
- Drake, J. M. 2005 Density dependent demographic variation determines extinction rate of experimental populations. *PLoS Biol.* **3**, 1300–1304.
- Drake, J. M. & Lodge, D. M. 2004 Effects of environmental variation on extinction and establishment. *Ecol. Lett.* **7**, 26–30.
- Duncan, R. P., Blackburn, T. M. & Sol, D. 2003 The ecology of bird introductions. *Annu. Rev. Ecol. Syst.* **34**, 71–98.
- Ebenhard, T. 1989 Bank vole (*Chethrionomys glareolus* (Schreber, 1780)) propagules of different sizes and island colonization. *J. Biogeogr.* **16**, 173–180.
- Forsyth, D. M. & Duncan, R. P. 2001 Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *Am. Nat.* **157**, 583–595.
- Gotelli, N. 1991 Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *Am. Nat.* **138**, 768–776.
- Haccou, P. & Iwasa, Y. 1996 Establishment probability in fluctuating environments: a branching process model. *Theor. Popul. Biol.* **50**, 254–280.
- Haccou, P. & Vatunin, V. 2003 Establishment success and extinction risk in autocorrelated environments. *Theor. Popul. Biol.* **64**, 303–314.
- Hanski, I. 1999 *Metapopulation ecology*. Oxford, UK: Oxford University Press.
- Hanski, I., Breukler, C. J., Schöps, K., Setchfield, R. & Nieminen, M. 2002 Population history and life history influence the migration rate of female Glanville fritillary butterflies. *Oikos* **98**, 87–97.
- Hartl, D. L. & Clark, A. G. 1997 *Principles of population genetics*, 3rd edn. Sunderland, MA: Sinauer Associates, Inc.
- Heino, M. & Hanski, I. 2001 Evolution of migration rate is a spatially realistic metapopulation model. *Am. Nat.* **157**, 495–511.
- Hubbell, S. 2001 *The unified neutral theory of biodiversity and biogeography*. Monographs in Population Biology, vol. 32 (ed. S. A. Levin & H. S. Horn). Princeton, NJ: Princeton University Press.
- Kareiva, P., Parker, I. M. & Pascual, M. 1996 Can we use experiments and models in predicting the invasiveness of genetically engineered organisms? *Ecology* **77**, 1670–1675.
- Kolar, C. S. & Lodge, D. M. 2001 Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**, 199–204.
- Leung, B., Drake, J. M. & Lodge, D. M. 2004 Predicting invasions: propagule pressure and the gravity of Allee effects. *Ecology* **85**, 1651–1660.
- Lockwood, J. L., Cassey, P. & Blackburn, T. 2005 The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* **20**, 223–228.
- MacIsaac, H. J., Borbely, J. V. M., Muirhead, J. & Graniero, P. A. 2004 Backcasting and forecasting biological invasions of inland lakes. *Ecol. Appl.* **14**, 773–783.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. A. 2000 Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710.
- Matis, J. H. & Kiffe, T. R. 2000 *Stochastic population models: a compartmental perspective*. Lecture Notes in Statistics, vol. 145. New York: Springer.
- Renshaw, E. 1991 *Modelling biological populations in space and time*. Cambridge Studies in Mathematical Biology, vol. 11 (ed. C. Cannings, F. G. Hoppensteadt & L. A. Segel). Cambridge, UK: Cambridge University Press.
- Ricciardi, A. 2001 Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? *Can. J. Fish. Aquat. Sci.* **58**, 2513–2525.
- Robinson, J. V. & Dickerson, J. E. 1987 Does invasion sequence affect community structure? *Ecology* **68**, 587–597.
- Robinson, J. V. & Edgemon, M. A. 1988 An experimental evaluation of the effect of invasion history on community structure. *Ecology* **69**, 1410–1417.
- Veltman, C. J., Nee, S. & Crawley, M. J. 1995 Correlates of introduction success in exotic New Zealand birds. *Am. Nat.* **147**, 542–557.