

Realized vs apparent reduction in enemies of the European starling

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Abstract

Release from parasites, pathogens or predators (i.e. enemies) is a widely cited ‘rule of thumb’ to explain the proliferation of nonindigenous species in their introduced regions (i.e. the ‘enemy release hypothesis’, or ERH). Indeed, profound effects of some parasites and predators on host populations are well documented. However, some support for the ERH comes from studies that find a reduction in the species richness of enemies in the introduced range, relative to the native range, of particular hosts. For example, data on helminth parasites of the European starling in both its native Eurasia and in North America support a reduction of parasites in the latter. However, North American ‘founder’ starlings were likely not chosen randomly from across Eurasia. This could result in an overestimation of enemy release since enemies affect their hosts on a population level. We control for the effects of subsampling colonists and find, contrary to previous reports, no evidence that introduced populations of starlings experienced a reduction in the species richness of helminth parasites after colonization of North America. These results highlight the importance of choosing appropriate contrast groups in biogeographical analyses of biological invasions to minimize the confounding effects of ‘propagule biases’.

Abbreviations: ERH – enemy release hypothesis; NIS – nonindigenous species

Introduction

An oft-cited explanation for the post-establishment proliferation of nonindigenous species (NIS) is that they leave behind many of their co-occurring enemies due to bottlenecks during the invasion process (Blossey and Nötzold 1995; Keane and Crawley 2002; Torchin et al. 2002, 2003; Mitchell and Power 2003; Torchin and Mitchell 2004). For invaders that become widespread and dominant, support for the generality of the ‘enemy release hypothesis’ (ERH *sensu* Keane and Crawley 2002) derives largely from studies that show a reduction in the number of enemy species in introduced relative to native ranges of their hosts (Mitchell and Power 2003; Torchin

et al. 2003). However, biogeographical patterns that support the ERH may be confounded by ‘propagule biases’ (Colautti and MacIsaac 2004; Colautti et al. 2004) because invading propagules, or ‘founders’, are unlikely to be truly random samples from across their native range. Therefore, the number of enemy species available to be introduced to new areas with their hosts may be much lower than that represented by the total number available from across the realm, provided that enemy distributions are spatially heterogeneous. Given this and other potential biases among patterns of enemy release, Colautti et al. (2004) proposed four categories of enemy release based on two classifications. First, a *release* from enemies requires some measure of the net effects

of enemies on the fitness or vigour of their host, or on their regulation of a given host population (e.g. Callaway et al. 2004; but see Agrawal and Kotanen 2003). Conversely, a number of other lines of support for the ERH come from studies that find a *reduction* in the species richness of enemies in the introduced range, without explicit tests for demographic or physiological release (e.g. Mitchell and Power 2003, Torchin et al. 2003, Torchin and Mitchell 2004). Patterns of enemy reduction may be further characterized as *apparent* or *realized* with the former referring to broad geographical comparisons (e.g. Eurasia vs North America) and the latter considering potential variation among populations within those regions. It may therefore be possible to test for propagule biases by comparing *apparent* and *realized* estimates of enemy reduction.

The European starling (*Sturnus vulgaris*) is a 'Stage V' invader (i.e. widespread and numerically dominant *sensu* Colautti and MacIsaac 2004), found throughout most of Canada and the United States (Long 1981). In spite of several failed attempts, a North American population was successfully established after Eugene Schieffelin released 80 and 40 birds into Central Park in New York City during 1890 and 1891, respectively (Long 1981). Previous studies have reported a reduction in the number of helminth parasites in introduced, North American populations relative to native, European ones (Dobson and May 1986; Torchin et al. 2003). Knowledge of the historical circumstances of starling introductions combined with an extensive parasitological literature render this an exemplary case with which to test for a propagule bias in one of the world's most widespread, pervasive NIS.

Materials and methods

Calculating 'realized' vs 'apparent' enemy reduction

Enemy reduction (R) of a host species has been quantified based on the number of enemy species in its native (N) and introduced (I) ranges such that $R = N - I$ (Mitchell and Power 2003; Torchin et al. 2003). This value can be standardized as a proportion of the total number of enemy spe-

cies in each region, such that $R = (N - I) / (N + I)$. We prefer this to the $(N - I) / N$ equation for proportional enemy reduction of Torchin et al. (2003) because ours does not assume that the number of enemies is always smaller in the introduced range. Thus, R may range from -1 to $+1$, with positive values supporting an enemy reduction and negative values indicating a net increase in enemies in the introduced range of the host.

To account for potential propagule biases, calculations for R can be separated into *apparent* and *realized* values, based on expected fitness effects (i.e. survival, reproduction, or vigour) on the host species. Therefore, it is the realized enemy reduction (R_{real}) on a population scale that may have potential effects on host fitness, as predicted by the ERH, rather than the apparent enemy reduction (R_{appt}) at a broad biogeographical scale. Thus, for Stage V invaders like the European starling, the ERH may be supported where $R_{\text{real}} \gg 0$, and refuted where $R_{\text{real}} \leq 0$ (Mitchell and Power 2003; Torchin et al. 2003, Torchin and Mitchell 2004). This of course assumes that host fitness in the introduced range is proportional to the number of co-occurring enemy species. It should be noted, however, that the true effect of enemies will not depend on species diversity *per se*, but on their overall impact on host fitness (Strauss and Agrawal 1999; Keane and Crawley 2002; Mitchell and Power 2003; Torchin et al. 2003). Data on helminth parasites are insufficient to test this assumption, nevertheless, comparing values of R_{appt} with R_{real} will show the degree to which previously reported patterns of enemy reduction may be confounded when contrast groups are not appropriately selected. Patterns of enemy reduction are artificially increased where $R_{\text{appt}} > R_{\text{real}}$, decreased where $R_{\text{appt}} < R_{\text{real}}$, and not confounded where $R_{\text{appt}} = R_{\text{real}}$. Propagule bias can therefore be discounted for the European starling if R_{appt} approximates R_{real} .

To test for inflated R_{appt} owing to parasite spatial heterogeneity in the homeland (i.e. a biogeographical propagule bias), we modelled the occurrence of helminth parasite species of the European starling using data from North America and Eurasia (Hair and Forrester 1970; Cooper and Crites 1976). Helminth species occurrences in these sources were typically categorized by region, usually country, which allowed us to

build a spatial model of parasite occurrence for all of Eurasia, as well as for three regions within the native range: (1) Great Britain; (2) Europe, excluding Britain and (3) The former Soviet Union (USSR). Similarly, we modelled the occurrence of helminth parasites for Canada and the United States (USA) separately, as well as North America as a whole.

History of introduction

Deliberate introductions of the European starling into North America are fairly well documented, including a number of failures dating back to 1872–1873 (Long 1981). Eugene Schieffelin was a co-founder of the American Acclimatization Society, whose mandate it was to introduce to North America all of the birds mentioned in the works of William Shakespeare (Long 1981; Lever 1992). Starlings were chosen for introduction owing to a single, unflattering passage in Henry IV, Part I; ‘I’ll have a starling shall be taught to speak nothing but “Mortimer,” and give it him to keep his anger still in motion.’ Historical data are insufficient to pinpoint the specific area from whence starlings were chosen for introduction to North America. However, two lines of evidence suggest an English or British source for Schieffelin’s birds. First, at the time of introduction, Liverpool was the major port for emigrants destined for North America, and the ubiquity of European starlings across Britain indicates that the species was likely available in the region surrounding Liverpool (Tiainen and Pakkala 1997). Second, an analysis of the types of parasites found in North America is most consistent with a colonist origin within or across Britain (see below). Nevertheless, genetic data are needed to confirm this assertion. Therefore, we also considered the possibility that other areas of Eurasia served as sources, and that unreported introductions of starlings were made in addition to Schieffelin’s.

Colonist subsampling

After controlling for a biogeographical propagule bias, we used a bootstrap approach to model the possibility that rare parasites are lost due to subsampling effects, thereby further increasing R_{appt} without necessarily affecting host fitness (i.e. a

subsampling propagule bias). Our bootstrap model was based on the assumption that the North American population of starlings was founded by a single introduction of 120 birds (Long 1981) drawn randomly from Wales. We used data from Wales (James and Llewellyn 1967) because it contained one of the most comprehensive surveys of starling helminth parasites, and because it most closely matched the parasite assemblages found in North America (see below). The exact number of birds chosen for introduction is not precisely known, but our assumption of 120 birds is the least likely to over-estimate R_{appt} when compared with other published accounts of starling introductions (see Long 1981 and references therein).

To test for a subsampling effect, we first generated random numbers from a negative binomial distribution fitted to the number of parasite species found in adult starlings (Owen and Pember-ton 1962). The negative binomial distribution explained a significant amount of deviance fitted by maximum likelihood (deviance = 9.08, d.f. = 1, $P = 0.003$) and has been used to describe parasite distributions in other studies (Shaw et al. 1998; Hudson et al. 2002). This produced a specific number of parasites for each of the 120 host birds; to determine which specific parasites were introduced for each bootstrap iteration, the percent incidence of the 11 parasites from James and Llewellyn (1967) were summed and the total was re-scaled to 100%. For each bird, a uniform random number was generated and parasite species were picked based on the scaled cumulative distribution for incidence. This process was repeated until the parasite species were matched to the number of species generated by the negative binomial distribution. For each group of 120 birds, the number of parasite species present was counted and the percent incidence calculated for each parasite. This process was repeated for 500 bootstrap iterations, from which we calculated a mean and standard error of the number of parasite species present among the 120 colonists, as well as the mean and standard error of percent incidence for each parasite species. To simulate two separate introduction events, we also ran separate simulations for 80 and 40 colonists and pooled the results. However, results were similar for both simulations, so we present here only results of the former.

Taxonomic ambiguity

Some parasites in our dataset occurred more than once, owing to taxonomic ambiguity. Where this occurred, we considered these multiple entries as a single species. For example, *Brachylaema fuscatus* and *B. fuscata* were considered as the same species, as were *Aploparaksis dujardini*, *Haploparaxis dujardini*, and *Rhabdometra nullicollis*. Another problem arose because some parasites were only identified to the genus level. For example, unspecified *Brachylaema* species were found in North America, which we considered to be *Brachylaema fuscata* because it is a common parasite throughout Eurasia and because there were no other *Brachylaema* species reported in the North American population. Combining genera like this could have overestimated the number of co-introduced parasites, but would equally underestimate host-switching in the native range. Thus, the net difference in the number of co-occurring enemies (i.e. R_{real} and R_{appt}) would not be affected.

Test for confounding factors

Independent of any model of parasite reduction, two factors could have confounded patterns of enemy occurrence in our dataset: variation in research effort conducted within each region, and the area of each region considered. A proper measurement of R_{real} requires comprehensive sampling of parasites from only the areas of founder source (presumably somewhere within Great Britain) and destination (presumably New York). However, the available data on parasite occurrence in these regions limits our ability to perform a statistically rigorous contrast. We therefore compared the median number of species found in each study in Canada, the USA, Britain, mainland Europe, and the USSR, using a Kruskal–Wallis (K–W) ANOVA based on recommendations in Sokal and Rohlf (2001).

High variance in research effort between studies could have restricted our ability to identify differences between regions. Much of this variance likely owes to drastic differences in sampling methods; for example James and Llewellyn (1967) examined 122 dead starlings, while Threlfall (1968) examined only four starlings. Additionally, a number of studies, particularly in

North America, identified only one or two new parasite species, without mention of other parasites. To compensate for the high degree of variability introduced by studies with weak sampling effort, and those reporting only new parasites, we re-ran the statistical analysis two additional times, first with the exclusion of studies reporting only one parasite species, and then again excluding those reporting only one or two species.

In a second attempt to control for variation in research effort, we pooled all helminth species for each region and divided by the number of studies. This provided us with an estimate of pooled, rather than average, regional helminth species diversity per unit research effort. To control for variation in study area between each group, we divided the number of parasite species by the log area for each region to calculate the number of parasites found per log km². We also contrasted species diversity and prevalence of helminth species in a study of Wales (James and Llewellyn 1967) with one of the New York area (Boyd 1951). These latter two approaches do not lend themselves to statistical analysis, but nonetheless provide valuable information on the diversity of helminth parasites in regions of Eurasia and North America.

Results and discussion

An examination of parasite species distribution in Eurasia revealed a great deal of heterogeneity in the distribution of parasites, particularly between eastern (USSR) and western (Britain) areas, although several species are shared between these regions (Figure 1). Three individual studies from three different regions of Eurasia had helminth parasite assemblages most similar to North America (Table 1): Wales (8 of 11 species were also reported in North America), northern England (9 of 16), and Leningrad (St. Petersburg), Russia (10 of 23). This strongly suggests that species were drawn from an area of parasite occurrence similar to, but perhaps more diverse than, Wales or northern England alone (i.e. likely somewhere in southern Britain). Therefore, the introduction can conservatively be modelled as a random selection of colonists from across all of Great Britain. The similarity of species found between Leningrad and North

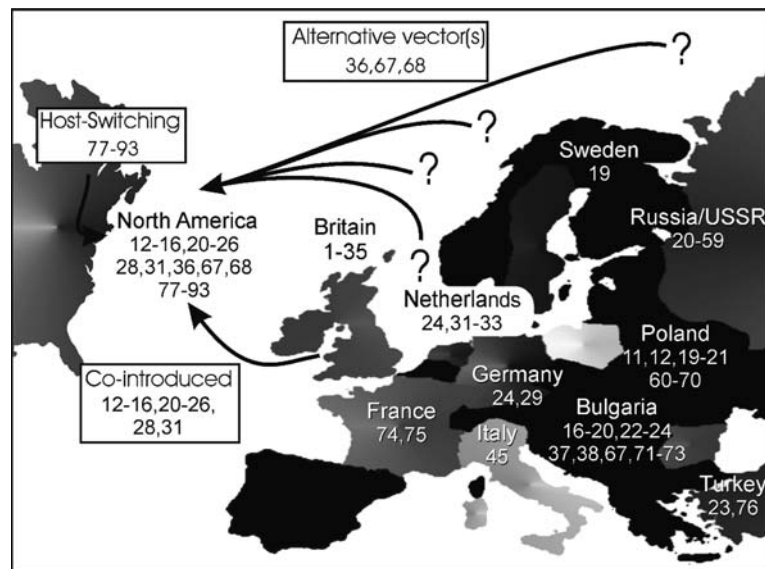


Figure 1. Spatial distribution of helminth parasites of the European starling. Each number represents a different parasite species. For example, 40 parasites are reported from Russia/USSR, 16 of which (species #20–35) are shared with Britain. Probable sources are given for helminth species found in North America: species that were co-introduced with starling colonists, those that invaded with other hosts, and parasites in North America that switched hosts. Four species are not included because they are only reported from India or Egypt, or because sampling locations were not specified (i.e. identified only as 'Europe').

America is initially surprising. However, all of the species common to Leningrad and North America are also found in Britain (Figure 1; Table 1). Thus, the parasite similarity between Leningrad and North America may be confounded by the similarity between Russia and Britain.

Our analysis reveals a great deal of geographic heterogeneity with respect to helminth diversity across Eurasia (Figure 1), raising the possibility that measurements of enemy reduction in the European starling have been confounded by propagule bias. This is further supported by comparison of enemy reduction between Eurasia (R_{apppt}) and Britain (a closer approximation of R_{real}). The starling population in North America has a net R_{apppt} of 0.31 based on calculations for Eurasia but a net R_{real} of -0.05 for Britain (Table 2). Thus, our estimate of R_{real} reveals both a strong propagule bias ($R_{\text{apppt}} \gg R_{\text{real}}$) and a net parasite increase ($R_{\text{real}} < 0$), in contrast to the decrease predicted by the ERH and previously argued for the European starling (Dobson and May 1986, Torchin et al. 2003). Our estimate may be conservative because it assumes that helminth species were drawn randomly from across all of Great Britain, but this comparison does

not control for differences in area or research effort.

Comparison of helminth communities identified in Wales and North America reveals a number of species that were likely not co-introduced with their host. For example, 3 of 11 parasite species found on starlings in Wales are not found in North America (Table 3). Torchin et al. (2003) used a bootstrap model on all helminth parasites across Eurasia and predicted a reduction in the number of enemies between Europe and North America. Our bootstrap model predicted a mean of $10.8 (\pm 0.5 \text{ SE})$ species from the pool of 11 due to colonist sampling effects. Thus, a subsampling of potential colonists appears unlikely to account for the reduction of parasite species in this case. More likely, the loss of a few parasite species owes to the low survival of highly infected birds, or the low survival of particular helminth species during transport or establishment of their host (see Torchin et al. 2002 for discussion and examples of other species).

Moreover, the incidences (i.e. proportion of birds infected) of helminth species in Wales do not correspond well with the species found in North America (Table 3). In other words, the incidence of helminth species on starlings in

Table 1. Helminth parasites found on starlings in North America (NA) and those shared with selected regions of Eurasia (EA): Wales (Wal), northern England (Eng), Leningrad (Len), Britain (Bri) and Europe (Eur).

Species	Source region						
	NA	Wal	Eng	Len	Bri	Eur	EA
<i>Brachylaema fuscata</i>	?	×	×	×	×	×	×
<i>Porrocaecum ensicaudatum</i>	×	×	×	×	×	×	×
<i>Variolepis farciminosa</i>	×		×	×	×	×	×
<i>Aploparaksis dujardini</i>	×	×	×	×	×	×	×
<i>Hymenolepis farciminosa</i>	×	×	×		×	×	×
<i>Capillaria contorta</i>	×		×	×	×	×	×
<i>Paricterotaenia parina</i>	×		×	×	×	×	×
<i>Choanotaenia muscicola</i>	×	×		×	×	×	×
<i>Leucochloridium cyanocittae</i>	×	×		×	×	×	×
<i>Capillaria caudinflata</i>	×	×			×	×	×
<i>Hymenolepis serpentulus</i>	×	×			×	×	×
<i>Capillaria exilis</i>	×		×		×	×	×
<i>Urogonimus certhiae</i>	×		×		×	×	×
<i>Capillaria ovopunctata</i>	×			×	×	×	×
<i>Microfilaria</i> sp.	?			?			?
<i>Conspicuum</i> sp.	?					?	?
<i>Dispharynx nasuta</i>	×					×	×
<i>Subuhura suctoria</i>	×					×	×
<i>Acuaria gracilis</i>	×						
<i>Anonchotaenia globata</i>	×						
<i>Capillaria columbae</i>	×						
<i>Choanotaenia iola</i>	×						
<i>Diplotriaena leilae</i>	×						
<i>Echinostoma revolutum</i>	×						
<i>Eufilaria</i> sp.	×						
<i>Lutztrema sturni</i>	×						
<i>Mediorhynchus grande</i>	×						
<i>Mediorhynchus robustum</i>	×						
<i>Microtetrameres helix</i>	×						
<i>Ornithodendrium imanensis</i>	×						
<i>Oxyspirura petrowi</i>	×						
<i>Plagiorchis noblei</i>	×						
<i>Plagiorhynchus formosus</i>	×						
<i>Splendidofilaria caperata</i>	×						
<i>Variolepis planestici</i>	×						
% of North American parasites in source	100	23	25	29	40	49	51
% of source parasites in North America	100	73	56	43	44	29	22

Parasites not identified to species level that might affect the number of shared and unique species are indicated by '?'.

Table 2. The number of helminth species (N_{spp}) identified in four regions of Eurasia, as well as Canada and the United States.

Region	N_{spp}	N_{studies}	Log area	$N_{\text{spp}}/N_{\text{studies}}$	$N_{\text{spp}}/\text{Log area}$	$N_{\text{spp}}/N_{\text{studies}}/\text{Log area}$	R_{appt}
All Eurasia	76	97	19.18	0.78	3.96	0.17	0.31
USSR	40	36	7.33	1.11	5.46	0.15	0.00
Britain mainland	36	31	5.39	1.16	6.68	0.22	-0.05
Europe	36	30	6.46	1.20	5.57	0.19	-0.05
North America	40	26	7.29	1.54	5.49	0.21	
Canada	7	4	7.00	1.75	1.00	0.25	
USA	39	22	6.97	1.77	5.59	0.25	

The number of studies (N_{studies}) and logarithm of land area (log area) are also indicated. Estimates of *apparent* enemy reduction (R_{appt}) of North American birds are shown for each region of Eurasia.

Table 3. Incidences of helminth parasites on adult and juvenile *Sturnus vulgaris* in northern England (Owen and Pember-ton 1962) and Wales (James and Llewellyn 1967).

Species	England	Wales	NA
Adults			
<i>Anomotaenia constricta</i>	1.3		
<i>Brachylaemus fuscata</i>	7.6	22.7	×
<i>Capillaria caudinflata</i>		5.7	×
<i>Capillaria contorta</i>	8.1		×
<i>Capillaria exilis</i>	48.4		×
<i>Choanotaenia muscolosa</i>		3.4	×
<i>Dilepis undula</i>	0.9	9.1	
<i>Aploparaxis dujardinii</i>	12.1	19.3	×
<i>Hymenolepis farciminosa</i>	55.6	2.3	×
<i>Hymenolepis serpentulus</i>		1.1	×
<i>Leucochloridium cyanocittae</i>		1.1	×
<i>Paricterotaenia parina</i>	17.0		×
<i>Polymorphus minutus</i>		4.6	
<i>Porrocaecum ensicaudatum</i>	8.5	29.5	×
<i>Prosthynchus cylindraceus</i>		70.5	
<i>Syngamus trachea</i>	14.3		
<i>Zonorchis petiolatus</i>	15.7		
Juveniles			
<i>Anomotaenia constricta</i>	0.7		
<i>Brachylaemus fuscatus</i>	5.2		
<i>Capillaria contorta</i>	23.0		×
<i>Capillaria exilis</i>	81.5		×
<i>Cyathostoma lari</i>	5.9		
<i>Dilepis undula</i>	12.6		
<i>Haploparaxis dujardinii</i>	5.9		
<i>Hymenolepis farciminosa</i>	54.8		×
<i>Paracterotaenia parina</i>	18.5		×
<i>Porrocaecum ensicaudatum</i>	43.0		×
<i>Prosthogonimus ovatus</i>	7.4		
<i>Prosthynchus cylindraceus</i>	2.2		
<i>Syngamus trachea</i>	67.4		
<i>Urogonimus certhiae</i>	0.7		×
<i>Zonorchis petiolatus</i>	14.8		

Species that are also found in North America (NA) are indicated by '×'. The study of European starlings did not examine incidences of juvenile birds.

Wales is not predictive of the species that successfully established in North America. These incidence rates were derived from a study of birds that were found dead, and, as such, may

not accurately reflect the incidences of live individuals, or those chosen for introduction. Furthermore, incidence rates for particular species likely vary spatially and temporally (Hudson et al. 2002). Comparison of incidences in northern England agrees much more closely with the particular species found in North America (Table 3). This is consistent with a source somewhere near Liverpool, which is geographically intermediate to the two studies. However, helminth data is insufficient to rule out other areas of Britain as possible sources.

Confounding variables

The most obvious limitation of our estimate of R_{real} is the well-known relationship between geographic area and the number of species found (Strong and Levin 1975; Clay 1995). This is undoubtedly an important consideration since North America is about 80 times the size of Great Britain. However there was no significant difference between the mean number of species per study for each of North America and Britain, or for any of the regions examined (Table 4). Differences between means may have been non-significant owing to the high variability in the research methods used, and thus the number of species identified in each study. However, means were not significantly different even after eliminating studies that identified only a single parasite, or those identifying only one or two ($P > 0.05$; Table 4). We also looked at the total number of species identified in each region to better understand the confounding effects of area.

The number of helminth species per log area in Britain ($6.68 \text{ spp}/\log \text{ km}^2$) was indeed higher than North America, or Canada or the USA alone (Table 2). However, the value for the USA was similar to the USSR and mainland Europe,

Table 4. Summary of Kruskal–Wallis ANOVA by ranks, showing the mean number of parasites per study for each region.

	Mean					P
	USSR	Europe	Britain	Canada	USA	
All studies	5.0	2.6	3.6	2	3.2	0.51
>One species	9.8	4.8	4.7	3	5.9	0.37
>Two species	11.8	6.2	5.8	3	6.9	0.07

The ANOVA was performed three times: (i) for all studies (All); (ii) excluding studies reporting only one species (>one species); and (iii) excluding studies reporting only one or two species (two species). None of the contrasts revealed significant differences ($P > 0.005$).

and was much larger than all of Eurasia combined (Table 2). Values varied most dramatically between Canada (1 spp/log km²) and the USA (5.59 spp/log km²). This disparity likely owes to the lower research effort in Canada (four studies) as compared to the USA (22 studies). Research effort may therefore be as or more important than area in confounding our results. After controlling for research effort, both Canada and the USA had similar values (1.75 and 1.77, respectively), and both were much higher than any area of Eurasia (Table 2). Finally, after controlling for both research effort and area, Canada and the USA had equal values and were higher than any region of Eurasia. However, North America as a whole had values similar to both Britain and mainland Europe (Table 2).

Finally, we contrasted two studies that examined helminth parasites in the likely source (Wales) and destination (New York) regions. James and Llewellyn (1967) found 11 helminth species among 122 dead starlings at a site in Wales. By comparison, Boyd (1951) identified 15 species among 300 starling individuals, the majority of which (61%) were shot live in New York State; several individuals were also taken from surrounding US states (Connecticut, Maryland, Ohio and Indiana). Differences in sampling effort, capture techniques, and area of study, make it difficult to draw conclusions about the helminth diversity of the two regions, although evidence for a decrease in diversity for the New York population is lacking. More importantly, combined prevalences of all helminth species were similar between both studies (85 and 90% for Wales and New York, respectively). While it is true that Boyd (1951) examined almost three times as many starlings as James and Llewellyn (1967), prevalence rates are relatively independent of sampling intensity when sample sizes are greater than about 100 individual hosts (Gregory and Blackburn 1991). Given the similarity in the number of species between North America and Eurasia, and the similar prevalences between the studies outlined above, there is no evidence for a reduction in the number of enemies between Britain and North America. Based on our analysis in Table 2, this pattern holds regardless of whether colonists were chosen randomly from Britain, mainland Europe, or the USSR. Finally, the R_{appt} calculated for Eurasia and North America is much higher than

that of North America and any region within Eurasia. These findings support the contention of Colautti et al. (2004) that previous estimates of enemy reduction in the European starling may have been confounded by a propagule bias.

Evidence for enemy release?

Some evidence supports the argument that starlings lose enemies from the native range during the invasion process and therefore may escape from their effects. Of 20 parasite species collectively reported in northern England and Wales, seven are absent from North America (Table 3). Three to five additional species found in Eurasia but not recorded in the two studies from northern England and Wales (Table 1) may have been co-introduced with other host species, or may have been introduced by additional, unrecorded introductions. The overall increase in parasites (i.e. negative value for R_{real}) thus owes primarily to the 17 parasite species that are found on starlings in North America, but not Eurasia (Table 1). Collectively, these species account for more than half of the parasites found on starlings in their introduced range, and likely represent host-switching of helminths native to North America. Of the five species found in Eurasia and North America but not northern England or Wales (Table 1), *Microfilaria*, *Conspicuum* and *Subulura* species were not identified to the species level in North America, thus their origins are uncertain. These genera, along with *Capillaria ovopunctata* and *Dispharynx nasuta*, may have been introduced with alternative hosts, or present in the area from whence colonists were chosen. For example, *D. nasuta* has a cosmopolitan distribution and infects numerous other bird species (Permin and Hansen 1998). In summary, starlings appear to have lost several particular helminth species, but this is apparently over-compensated by host-switching of helminth species in the bird's introduced range. In retrospect, this may not be surprising since starlings represent naïve hosts to these parasites (Colautti et al. 2004). If enemy interactions are an important factor regulating the abundance and impact of the European starling, our results caution that the effects of helminth enemies do not simplify to a relationship between enemy diversity and 'invasiveness'.

Propagule biases and enemy reduction

The high degree of parasite occurrence in native and introduced populations of the European starling (Figure 1) support the hypothesis that propagule biases have confounded patterns of enemy reduction reported for this species. Propagule biases associated with the biogeographical subsampling phenomenon identified herein could also confound similar patterns of enemy reduction reported in other stage V invaders (e.g. Dobson and May 1986; Torchin et al. 2002; Mitchell and Power 2003; Torchin et al. 2003; Torchin and Mitchell 2004). If so, R_{appt} is expected to be highest where a host species has a widespread distribution in its native range and where enemy occurrence is highly heterogeneous. This bias could also lead to spurious correlations between enemy reduction and 'invasiveness', since widespread NIS tend to be those that are widely distributed elsewhere (Goodwin et al. 1999; Blackburn and Duncan 2001). Greater attention must therefore be given to this possibility when investigating possible instances of enemy release.

Recent biogeographical evidence supports an overall reduction in the number of enemies in introduced relative to native ranges (Dobson and May 1986; Torchin et al. 2002; Mitchell and Power 2003; Torchin et al. 2003). However, several 'common garden' experiments suggest that many NIS of host are equally, or more, susceptible to attack from enemies than are native host species within the same community (Blaney and Kotanen 2002; Agrawal and Kotanen 2003). These results suggest a biogeographical pattern of reduced enemies that may not be borne out at the community level (Colautti et al. 2004). One possibility is that biogeographical differences in the number of enemies are confounded by propagule bias, although this is certainly not the only possible explanation. This hypothesis is supported by our finding of a high R_{appt} between Eurasia and North America relative to R_{appt} calculated for North America and regions within Eurasia, which are closer estimates of R_{real} (i.e. $R_{\text{appt}} - R_{\text{real}} \gg 0$); that is, an apparent reduction of enemies with no realized decrease in the number of helminth enemies at a population level.

To avoid propagule biases, a more comprehensive re-evaluation of enemy reduction in the European starling and other species will likely

require the identification of 'invasion pathways' to pinpoint invasion sources (Ricciardi and MacIsaac 2000). For example, averaged, pairwise comparisons between particular surveys will solve the problem of biogeographical heterogeneity in enemy occurrence, but could still be confounded if the proper source region is not identified. A random sample of all studies would reduce the potential for an inflated R_{appt} , but could still artificially increase R_{appt} if enemies were included from regions that were not colonist sources. Where historical data is ambiguous or unavailable, genetic markers may aid in identifying putative invasion sources (e.g. Cristescu et al. 2001).

Our analysis of propagule biases also exposes the problem of human perception in biogeographical studies of biological invasions. The European starling is widespread, forms large aggregating populations, and is considered a nuisance to farmers in both its native and introduced ranges (Long 1981), yet is typically considered as 'invasive' only in the latter. A biogeographical approach will undoubtedly provide important insights beyond those from taxonomic contrasts that are now commonplace in the invasion literature (e.g. Goodwin et al. 1999). However, our findings highlight the importance of identifying appropriate contrast groups when assessing changes in populations of Stage V invaders at a biogeographical scale.

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