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What are the consequences of infection by the introduced parasite *Philometroides sanguineus* for threatened crucian carp *Carassius carassius* populations in England?

Josephine Pegg[1], Chris F. Williams[2], Julien Cucherousset[1,3,4], J. Robert Britton[1]
[1]Centre for Conservation Ecology and Environmental Sciences, School of Applied Sciences, Bournemouth University, Poole, Dorset, UK
[2]Environment Agency, Bromholme Lane, Brampton, Cambridgeshire, UK
[3]CNRS, UPS, ENFA; UMR5174 EDB (Laboratoire Évolution et Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France
[4]Université de Toulouse, UPS, UMR5174 EDB, F-31062 Toulouse, France

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Abstract – Nonnative parasites have the potential to detrimentally affect naïve hosts, resulting in negative consequences for their growth, condition and energetics. Here, the effect of the introduced parasitic nematode *Philometroides sanguineus* on crucian carp *Carassius carassius* populations in England was investigated. Populations of *C. carassius* populations are increasingly spatially restricted in England and under increasing threat from habitat loss and hybridisation. Parasite prevalence across 6 infected populations was <27% and, generally, there was no significant relationship between levels of infection and fish length and age. Parasite abundance ranged between 1 and 8 nematodes and was not significantly related to fish length and age. Comparison of the growth, body weight and condition, and energy reserves between infected and noninfected *C. carassius* revealed infection did not incur significant detrimental impacts on these parameters. Whilst this suggests that infection had only minimal impacts on the examined host fish, this may have been a consequence of a low proportion of fish <100 mm in samples (i.e., size-selective effects) and some tests did suffer from low statistical power because of, for example, unbalanced sample sizes. It does, however, suggest that *P. sanguineus* may not be a major threat to the status of these *C. carassius* populations and infection by introduced parasites may not always incur significant impacts in naïve fishes.

Key words: *Philometroides sanguineus*; *Carassius carassius*; parasite prevalence; parasite abundance

Introduction

The introduction of alien species into new ecosystems is a major ecological issue that can have profound effects on biodiversity (Rahel & Olden 2008). An inherent and persistent risk associated with such introductions is the concomitant release of alien pathogens that may infect naïve hosts in the receiving area (Peeler et al. 2011). This is particularly concerning in aquatic environments where disease transfer has led to serious and irreversible effects upon native communities, including fish, such as the introduction of *Gyrodactylus salaris* into Norway that caused declines in native Atlantic salmon *Salmo salar* populations (Johnsen & Jensen 1988). Despite these apparent risks, not all alien pathogens may have obvious detrimental effects on naïve hosts and populations, although this may be related to difficulties in the measurement and evaluation of sub-lethal effects in wild populations. Consequently, the impact of many introduced parasites on native host populations remains unclear and requires clarification (Kennedy 1994; Blanc 1997; Hedrick 1998).

Correspondence: J. Robert Britton, Centre for Conservation Ecology and Environmental Sciences, School of Applied Sciences, Bournemouth University, Poole, Dorset BH12 5BB, UK. E-mail: Rbritton@bournemouth.ac.uk

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The introduction of alien fish pathogens is generally accidental, resulting from aquaculture activities such as fish imports and subsequent in-country movements (Kirk 2003; Gozlan et al. 2009; Peeler et al. 2011). The accidental nature of parasite release and their subsequent high potential for rapid dissemination through fish stocking activities or water transfer means their distribution and dispersal is difficult to regulate and manage (Hickley & Chare 2004). The precautionary approach is usually adopted for the risk management of unintentional alien introductions (Convention on Biological Diversity 2010) and is highly applicable to alien pathogens. This is because studies on their role in structuring native fish populations are limited, being generally restricted to those pathogens that have sudden or obvious impacts on host populations (e.g., mortality) (Gozlan et al. 2009). Consequently, there is a paucity of knowledge on many introduced fish pathogens, and in such cases, precaution has to be used to underpin control measures to protect native aquatic environments rather than using evidence-based science (Hickley 2009).

In England, crucian carp *Carassius carassius* is native to central and southern regions but is increasingly threatened by factors including habitat loss and loss of genetic integrity through hybridisation with introduced fishes (Wheeler 2000; Hänfling et al. 2005). Although the species is not threatened across their entire range, recent work has emphasised the requirement to conserve their remaining populations in England (e.g., Copp et al. 2008; Tarkan et al. 2009) and so the species increasingly appears in regional Biodiversity Action Plans (BAP; e.g., Copp & Sayer 2010; Lambeth Council 2010). However, such conservation efforts may be compromised by infections of introduced pathogens (Lilley et al. 1997; Kirk 2003). Literature suggests that the parasitic nematode *Philometroides sanguineus* represents an additional pressure on their populations. This parasite, specific to fish of the genus *Carassius* (Moravec 1994), is transmitted to *C. carassius* via ingestion of free-living parasitised copepods, the intermediate host (Yashchuk 1971; Moravec 1994; Anderson 2000; Wang 2002). Male and unfertilised female nematodes initially remain localised on the wall of the swim bladder and cause little obvious damage. After copulation, however, female worms migrate through the musculature into the fins from late summer, with intensities increasing during autumn and winter, and they increase in length to a maximum of 50 mm (Wierzbicki 1960). They remain in the fins until temperatures increase in spring when they liberate their larvae through the process of 'functional bursting' (Yashchuk 1971; Moravec 1994). Thus, the migration of gravid females into the fins and the subsequent emergence of larvae have the potential to cause substantial tissue damage and their development may make substantial energetic demands on the host. Their effects are generally more obvious in smaller hosts, with evidence of gross abnormalities in fish measuring <60 mm (Vasilkov 1983; Moravec 1994). By contrast, males remain on the swim bladder at lengths below 3 mm and do not result in any gross pathological damage. In England, the parasite is known to infect at least seven *C. carassius* populations. Whilst it is believed to be an introduction to the parasitic fauna of British freshwater fish, the source of the introduction remains unclear. The introduction of *P. sanguineus* to other countries has been associated with movements of infected goldfish *Carassius auratus* L. within the ornamental fish industry (Moravec 1994) and imports of infected cyprinid fish for aquaculture (Moravec & Cervinka 2005).

Whilst the pathology of infection in *C. carassius* is now being increasingly understood (Williams et al. in press), it is not yet known how this translates into sublethal impacts on ecological parameters such as growth, condition and energetics. Yet, these are crucial data for assessing the consequences of infection for parasitised individuals and would assist understanding of whether infection further threatens *C. carassius* populations in England. Consequently, the aim of the study was to quantify, using the *P. sanguineus*: *C. carassius* parasite: host system, the ecological consequences of infection by an introduced parasite on a naïve fish through evaluation of parasite prevalence and abundance, and the associated impacts on the infected host fish when compared to their noninfected con-specifics.

Materials and methods

Sample collection

Samples of fish from *C. carassius* populations known to be infected with *P. sanguineus* were initially collected from five lakes in England between October 2003 and May 2004. This timing was to coincide with the peak period for the presence of mature female nematodes within the fins and the period during which the host energetic demand may be at its greatest (growth and development of the mature female). Following capture with a 25- and 50-m micromesh seine net, samples were taken to the laboratory where they were euthanised by lethal anaesthesia (5% w/v benzocaine), measured (fork length, L, mm) and weighed (W, nearest 0.001 g). Fins were examined under a low power dissection microscope for the presence of mature female parasites; where detected, their size, position and location was noted. An ex- and internal parasitological examination was then undertaken to identify the presence of any other infections that may have confounded subsequent analyses that assessed the status of infected and noninfected fish;

in all cases, there were no other significant infections detected. A further sample of *C. carassius* was obtained from a newly detected site in March 2005 (where all fish were removed following pond draining) and then from Site 5 (cf. Table 1) in April 2010; these fish were euthanised in the laboratory and then analysed. In both cases, the data collected were as previously described but with the additional collection of scales to enable subsequent age estimations, and the dissection and weighing (nearest 0.001g) of the gonad and liver of each fish. It should be noted that in all cases, water names and locations cannot be provided for reasons of business confidentially.

Data analysis

For the samples collected in 2003 and 2004, data were analysed for mean lengths (±standard deviation, SD) of all fish, noninfected and infected fish, parasite prevalence (proportion of infected fish, %), parasite abundance (number of parasites per fish) and condition of individual fish (K, where $K = 100 \times W/l^3$, where length was measured in cm). Mean lengths were compared between the groups (infected vs. noninfected fish) using ANOVA, and differences in condition between the groups were analysed using ANCOVA where the allometric effect of body length was controlled as a covariate. In these and all subsequent ANCOVA tests, outputs were the significance of the difference between the group means, the equality of variances, homogeneity of regression slopes, partial eta squared (×100) and posthoc power analysis. Differences between group means were assessed at $\alpha = 0.05$. Equality of variances was measured using the Levene's test where $P > 0.05$ indicated equal variances between the groups. Homogeneity of the regression slopes was used to ensure there was no interaction between the covariate (fish length) and the groups (infected and noninfected fish), with this indicated when $P > 0.05$. Partial eta squared (ηp^2) was used to indicate group differences that were independent of sample size (effects size), where increased values indicated a greater group effect. The posthoc power analysis indicated the power of the test to detect a statistical difference between the groups. These tests were completed in SPSS v. 16.0 (IBM Corporation 2010, Somers, NY, USA).

For the samples collected in March 2005 and April 2010, the effects of infection on the parameters of growth (somatic and gonad), body weight, condition (K) and energy reserves were also assessed. Where sample sizes were large, sub-samples of fish were used to derive these parameters; these comprised of an equal number of infected and noninfected fish to provide balanced samples for statistical testing. Determining somatic growth required the age of fish to be initially assessed by analysing scales under a projecting microscope (×20) and counting the number of annuli. Fish growth was then compared between the groups of noninfected and infected fish by comparing residuals of length-age regressions to examine differences between the two groups. This method was used because of statistical complications resulting from reliance on back-calculated lengths, i.e., repeated measurements from individual fish. To estimate mean fork length and identify differences in growth between infected and noninfected fish, linear regressions of back-calculated fork length on age were completed and residuals stored. Species-specific mean residual values, as mean fork length adjusted for age, were then compared between the two groups (ANOVA). Gonad growth (females only) was assessed through gonad weight and the gonado-somatic index (GSI), calculated by (gonad weight/somatic weight) × 100, where somatic weight was total weight minus gonad weight. Energetic reserves were assessed using liver weight and the hepatic-somatic index (HSI), calculated from (liver weight/body weight) × 100, where body weight was total weight minus liver weight. On completion, their data were tested for normality and log-transformed where necessary before ANCOVA models were constructed to test the effects of infection on the parameters by controlling the allometric effect of fish length. These models were only deemed valid when the assumptions were met that variances were equal between the groups (Levene's test) and there was no interaction between the covariate and the groups (homogeneity of the regression slope). Where these assumptions were not met, then the output

Table 1. Sample size, parasite prevalence and abundance, and comparative mean lengths and their ANOVA output, of *Carassius carassius* populations infected with *Philometroides sanguineus* in the initial samples from Sites 1 to 5 collected in 2003 and 2004.

Site number	Sample size (n)	Number parasitized fish (parasite prevalence)	Range of parasite abundance (mean)	Mean length all fish (mm; ±SD)	Mean length non-infected fish (mm; ±SD)	Mean length infected fish (±SD)	Significance of difference in mean length (ANOVA)
1	69	12 (17.4%)	1–2 (1.1)	84 (20)	82 (19)	93 (21)	$F_{1,67} = 3.26$, $P > 0.05$
2	39	5 (12.8%)	1–2 (1.2)	113 (23)	112 (24)	118 (23)	$F_{1,37} = 0.35$; $P > 0.05$
3	155	15 (9.7%)	1–4 (1.9)	110 (67)	103 (65)	168 (48)	$F_{1,153} = 13.98$; $P < 0.01$
4	14	3 (21.4%)	1–2 (1.3)	133 (34)	127 (35)	154 (22)	$F_{1,12} = 1.67$; $P > 0.05$
5	90	9 (10.0%)	1–2 (1.1)	138 (20)	138 (20)	141 (18)	$F_{1,88} = 0.22$; $P > 0.05$

of the test was not considered further. Where transforming variables were unsuccessful in producing normally distributed data and the relationship between that parameter and fish length was not significant, a Mann–Whitney test was used to test for significant differences between the groups.

Results

Infections of *P. sanguineus* were present in all of the initial five samples of the *C. carassius* populations sampled in 2003 and 2004 (Table 1). Parasite prevalence ranged between 9 and 21%, and parasite abundance between 1 and 4 nematodes (mean intensity 1–1.9 worms per host) (Table 1). In all except Site 3, there was no significant difference in the length of infected and noninfected fish (Table 1); in Site 3, infected fish were significantly larger. ANCOVA was used to test for differences in condition between infected and noninfected fish in each site and revealed differences were not significant in Sites 2–5 (Table 2). Whilst the power of these tests were all <0.8, effect sizes (ηp^2) were generally low, indicating a relatively small influence of infection on condition. The exception was Site 1 where there was a significant difference in condition between infected and noninfected fish (Table 2). However, pairwise comparisons based on estimated marginal means and adjusted for multiple comparisons (Bonferroni) revealed that it was the infected fish that were significantly higher in condition (infected: 1.87 ± 0.04, noninfected: 1.63 ± 0.02; $P < 0.01$).

The sample of *C. carassius* collected in April 2010 from Site 5 (cf. Table 1) comprised 221 fish of which 45 were infected with *P. sanguineus* (20%), indicating persistence of the parasite approximately 6 years after their initial detection in the site. Parasite abundance now ranged between 1 and 4 and the majority of infected fish were host to only one parasite (73%). Scale ageing of 90 fish (45 infected and 45 randomly selected noninfected fish) revealed individuals present in both groups between age 0+ and 7+ years. Comparison of their age-adjusted mean lengths (residuals of regression of length on age; ANOVA) showed no difference in mean back-calculated lengths at age between the infected and noninfected fish ($F_{1,88} = 1.19$, $P > 0.05$). In this sub-sample, there was also no significant difference in body weight, condition and liver weight between the infected and noninfected groups when the allometric effects of fish length were controlled (Table 3). Posthoc power analysis revealed statistical power was <0.8 in the tests, although effect sizes (ηp^2) were low, indicating a

Table 2. Comparison of the condition (*K*) of non-infected *Carassius carassius* and those infected with *Philometroides sanguineus* (ANCOVA) in the initial samples from Sites 1 to 5 collected in 2003 and 2004, where the allometric effect of fish length was controlled in the model. Sample sizes are provided in Table 1.

				ANOVA output				
Site number	Mean condition all fish (±SD)	Mean condition non-infected fish (±SD)	Mean condition infected fish (±SD)	Significance of equality of variances (*P*)	Homogeneity of regression slope (Group vs. fish length)	Partial eta squared (×100)	ANOVA output (infection × condition)	*Post-hoc* power of test
1	1.67 (0.17)	1.62 (0.15)	1.88 (0.09)	0.25	$F_{1,65} = 2.21$; $P > 0.05$	9.79	$F_{1,65} = 7.06$; $P = 0.01$	0.77
2	1.99 (0.15)	1.98 (0.14)	2.11 (0.21)	0.36	$F_{1,35} = 0.19$; $P > 0.05$	0.10	$F_{1,35} = 0.02$; $P > 0.05$	0.05
3	2.08 (0.29)	2.1 (0.26)	2.26 (0.25)	0.07	$F_{1,151} = 3.62$; $P > 0.05$	2.11	$F_{1,151} = 3.26$; $P > 0.05$	0.49
4	1.90 (0.17)	1.94 (0.14)	1.81 (0.25)	0.64	$F_{1,10} = 3.12$; $P > 0.05$	3.01	$F_{1,10} = 4.3$; $P > 0.05$	0.47
5	1.87 (0.12)	1.86 (0.12)	1.89 (0.16)	0.64	$F_{1,86} = 0.24$; $P > 0.05$	5.1	$F_{1,86} = 1.12$; $P > 0.05$	0.57

Table 3. ANCOVA outputs for Site 5, sampled in April 2010 (cf. Materials and methods), testing the influence of infection by *Philometroides sanguineus* (Group) on *Carassius carassius* parameters relating to body weight (g), condition (*K*) and energetics (as liver weight), where the allometric effects of fish length were controlled; model outputs are only shown for tests where all assumptions were met (cf. Materials and methods).

Parameter	Mean parameter all fish (±SD) ($n = 90$)	Mean parameter uninfected fish (±SD) ($n = 45$)	Mean parameter infected fish (±SD) ($n = 45$)
Body weight (log-transformed)	1.65 (0.24)	1.59 (0.27)	1.70 (0.18)
Condition (*K*)	1.79 (0.14)	1.77 (0.12)	1.84 (0.10)
Liver weight (g)	1.37 (0.20)	1.32 (0.20)	1.43 (0.18)

Parameter	Significance of equality of variances (*P*)	Homogeneity of regression slope (Group vs. fish length)	Partial eta squared (×100)	ANOVA output (effect of infection on parameter)	*Post-hoc* power of the test
Body weight (log-transformed)	0.25	$F_{1,88} = 1.34$, $P > 0.05$	3.2	$F_{1,88} = 2.13$, $P > 0.05$	0.30
Condition (*K*)	0.07	$F_{1,88} = 0.79$, $P > 0.05$	1.2	$F_{1,88} = 0.79$, $P > 0.05$	0.44
Liver weight	0.90	$F_{1,88} = 1.10$, $P > 0.05$	6.4	$F_{1,88} = 1.10$, $P > 0.05$	0.54

small group effect on the parameters (Table 3). Logarithmic transformation of HSI was unsuccessful in producing normal distributed data; as its relationship with fish length was not significant ($R^2 = 0.21$; $F_{1,88} = 3.16$, $P > 0.05$), then a Mann–Whitney test was used and revealed the effect of infection on HSI was not significant ($Z = -1.662$, $P > 0.05$).

The sample collected in March 2005 from the newly detected population provided a total sample size of 828 *C. carassius* of which 226 were infected with *P. sanguineus* (27%), with the majority of parasites recorded in the caudal fin. Noninfected fish were between 29 and 206 mm, and infected fish between 55 and 204 mm; there was no significant difference in length between the infected and noninfected groups (ANOVA: $F_{1,826} = 0.06$, $P > 0.05$). Regarding parasite abundance, 59% of the infected fish had only 1 parasite present, with the maximum number recorded in an individual fish being 8. The relationship between length of infected fish and parasite abundance was not significant (ANOVA: $F_{1,225} = 2.03$, $P > 0.05$). Ageing scales from 100 fish (50 infected, 50 noninfected, both randomly selected) revealed fish in both groups present at ages 0+ to 5+ years. Comparison of their age-adjusted mean lengths (residuals of regression of length on age; ANOVA) showed no difference in mean lengths at age between the groups ($F_{1,98} = 1.29$, $P > 0.05$). There was no significant difference in body weight, condition and gonado-somatic index between the groups when the effects of fish length were controlled in ANCOVA (Table 4). Whilst posthoc power analysis revealed statistical power in the tests was <0.8, effect sizes (ηp^2) were low, suggesting a small group effect on the parameters (Table 4).

Discussion

Parasitism of *C. carassius* by *P. sanguineus* resulted in relatively low prevalence (<27%), and the majority of infected fish had only 1 gravid female in their caudal fin. The outputs of subsequent analyses suggested these infections of *P. sanguineus* in *C. carassius* were insufficient to incur significant negative impacts on the growth (somatic and gonad), body weight, condition and energy reserves of infected host fish. In the context of current conservation threats to populations of *C. carassius* in England, including habitat loss (Copp et al. 2008) and genetic introgression with nonnative cyprinid fishes (Hänfling et al. 2005), the risk of this parasite causing further damage to threatened populations appears relatively low. Our findings indicate that the disease risk assessment for *P. sanguineus* in England no longer has to rely on precautionary principles. The data presented here, in conjunction with data from histopathology (Williams et al. in press), will enable the development of evidence-based assessment methods for managing risk to native fishes.

Evidence from this study that the impacts of *P. sanguineus* on *C. carassius* are not significant does, however, have caveats in relation to statistical power of tests and the size ranges of fish examined. Regarding statistical power, in the ANCOVA tests, the posthoc power analyses indicated relatively low power as a consequence of, for example, unbalanced sample sizes (Sites 1–5, sampled in 2003 and 2004). This was, however, partially countered by testing for the effect of group size on the mean differences between the infected and noninfected fish. These values were generally low, supporting the inference that infection was not having a substantial negative effect on these fish. These statistical issues do, however, indicate the problems that can be encountered when reliant on wild fish populations for parasite studies where information on sample sizes and the proportion of parasitised fish are unknown in advance and may be unbalanced. Regarding fish size, previous studies have suggested that gross abnormalities from infection by *P. sanguineus* are most apparent

Table 4. ANOVA outputs for the site sampled in March 2005 (cf. Materials and methods) testing the influence of infection by *Philometroides sanguineus* (Group) on *Carassius carassius* parameters relating to body weight (g), condition (*K*) and reproductive effort (as gonadosomatic index of female fish), where the allometric effects of fish length were controlled; model outputs are only shown for tests where all assumptions were met (cf. Materials and methods).

Parameter	Mean parameter all fish (±SD) ($n = 100$)	Mean parameter uninfected fish (±SD) ($n = 50$)	Mean parameter infected fish (±SD) ($n = 50$)
Body weight (log-transformed)	1.55 (0.31)	1.48 (0.39)	1.61 (0.20)
Condition (*K*)	1.86 (0.15)	1.82 (0.14)	1.89 (0.14)
Gonado-somatic index (females only)	2.01 (0.48)	1.90 (0.50)	2.10 (0.30)

Parameter	Significance of equality of variances (*P*)	Homogeneity of regression slope (Group vs. fish length)	Partial eta squared (×100)	ANOVA output (effect of infection on parameter)	*Post-hoc* power of the test
Body weight (log-transformed)	0.08	$F_{1,98} = 1.91$, $P > 0.05$	16.4	$F_{1,98} = 6.48$, $P < 0.02$	0.70
Condition (*K*)	0.50	$F_{1,98} = 2.12$, $P > 0.05$	12.9	$F_{1,98} = 2.37$, $P > 0.05$	0.58
Gonado-somatic index (females only)	0.09	$F_{1,48} = 0.91$, $P > 0.05$	3.3	$F_{1,48} = 1.10$, $P > 0.05$	0.18

in fish measuring <60 mm (Vasilkov 1983; Moravec 1994) and so would be expected to incur greater energetic costs compared with noninfected fish of the same length. Records of host debilitation and mortality in other fish species as a result of philometrid parasites highlight the susceptibility of juvenile fish to these nematodes (Vasilkov, 1967; Sinderman 1987; Moravec 1994). The proportion of infected fish of <60 mm was low in this study and, correspondingly, should samples have comprised a greater proportion of smaller fish then significant impacts may well have been detected. This suggests that future work should concentrate on the impacts of infection in these size classes in conjunction with controlled laboratory experiments that enable greater elucidation of impacts through the elimination of potential confounds and increasing the statistical power of subsequent tests. Notwithstanding, in Site 5, there was no evidence to suggest that any infection of juvenile *C. carassius* by *P. sanguineus* had incurred mortality sufficient to severely inhibit recruitment and threaten the sustainability of their population, as the age structure in 2010 comprised of fish in age classes between 1 and 7 years, approximately 6 years after their initial detection on the site.

The Philometrid group of parasites are, however, generally highly pathogenic parasites, responsible for disease outbreaks in both wild and farmed fish populations (Sinderman 1987; Moravec 1994). However, there are only limited detailed data available on their prevalence and pathogenicity in the wild (Moravec 1994, 2006) with little information on their sublethal effects (de Buron & Roumillat 2010). Thus, this study represents an important step in better understanding the impacts of infections of *P. sanguineus* on naïve hosts. Moreover, this study provides context on the issue of introduced parasites on naïve fish hosts and those in other animal groups. Other studies strongly suggest that impacts of introduced parasites are generally severe. For example, the Asian fish tapeworm *Bothriocephalus acheilognathi*, a parasite that has been introduced around the world through the aquaculture trade (Salgado-Maldonado & Pineda-Lòpez 2003), has been responsible for high mortality rates in cultivated cyprinid fish and has had pathogenic effects in wild populations (Bauer et al. 1973; Clarkson et al. 1997). The eel swim-bladder nematode, *Anguillicoloides crassus*, introduced from Asia into Europe, has incurred severe ecological consequences as it has spread rapidly through Europe, Africa and America (Kirk 2003). Infections of the European eel *Anguilla anguilla* have severely impaired swim-bladder function and caused mortalities in populations when in the presence of other stressors (Kirk 2003). In other animal groups, parasitism of juvenile ground finches *Geospiza fortis* in the Galápagos Islands by introduced *Philornis downsi* resulted in increased mortality and was concluded to have the potential to lead to large population declines (Huber 2008).

In summary, infection by *P. sanguineus* appeared not to have serious ecological implications for threatened *C. carassius* populations in England, a contrast with many other introduced parasite-naïve host systems, although further work is necessary to quantify their effects on smaller individuals. This work highlights the need for clear pathological, epidemiological and ecological data to evaluate disease risks from introduced parasites.

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