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Parasite-mediated competition between pheasant and grey partridge: a preliminary investigation

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Abstract Pheasants (*Phasianus colchicus*) and grey partridges (*Perdix perdix*) were maintained together on land known to be contaminated with eggs of the caecal nematode *Heterakis gallinarum* to examine the hypothesis that this shared parasite has a greater impact on grey partridges than on pheasants. Since an inverse relationship between worm intensity and partridge body condition was detected, while no such relationship with pheasant body condition was observed, we were unable to refute this hypothesis. Furthermore, that there was no relationship between worm intensity after the exposure period and partridge body mass prior to the infection trial implies that infection caused the decrease in partridge body condition, and not vice versa. Data consistent with previous observations that *H. gallinarum* fecundity and survival is greater in pheasants than in partridges suggest that the bulk source of nematode infection to wild grey partridges is reared pheasants, and not the partridges themselves. This, and the differential impact on host body condition, supports the hypothesis that the spread of parasites from increasing numbers of released pheasants has contributed to the decline in wild grey partridge populations in the UK within the past 50 years.

Key words Apparent competition · *Heterakis gallinarum* · Nematode · *Perdix perdix* · *Phasianus colchicus*

Introduction

The number of wild grey partridge (*Perdix perdix*) has declined dramatically in Europe within the past 50 years

(Potts 1986). This decline has been linked with changes in agricultural practices in general (Sotherton 1998) and, more specifically, a decrease in the abundance of invertebrate food for chicks due to herbicide and pesticide application (Southwood and Cross 1969; Rands 1985; Potts and Aebischer 1994). Grey partridge abundance, however, has also decreased in upland regions where agricultural practices have remained relatively unchanged and application of herbicides is uncommon. Thus, additional factors must also be involved in their decline.

During the period that grey partridge abundance has declined in the UK, the number of pheasants (*Phasianus colchicus*) reared and released on private sporting estates has increased dramatically (Tapper 1992). This inverse relationship between the two species highlights the possibility that adverse interactions with released pheasants may have contributed to the decline in the grey partridge population. One mechanism by which this may have occurred is 'apparent' competition via the shared parasites of the two gamebird species (Wright et al. 1980; Kimmel 1988; Robertson 1996). When two host species share the same parasites, the more resistant host can be a superior competitor by simply harbouring and transmitting those parasites to the more vulnerable host (Holt and Lawton 1994; Hudson and Greenman 1998).

Pheasants and grey partridges share a range of gastrointestinal nematodes by which apparent competition may be mediated (Keymer et al. 1962). One of the most likely candidates is the caecal worm *Heterakis gallinarum* which is by far the most abundant worm infecting pheasants in the UK (Hillgarth 1990), and which also regularly infects grey partridges (Clapham 1935). *H. gallinarum* is known to cause tissue damage in the caeca of its hosts (Kanshik and Deorani 1969), and its infective egg stage can act as a carrier for the pathogenic protozoan *Histomonas meleagridis*, the causative agent of 'blackhead' (Ruff et al. 1970).

In this paper, we examine the hypothesis that the shared caecal nematode *H. gallinarum* has a greater im-

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fect on grey partridges than on pheasants. Specifically, we test the prediction that partridge body condition and intensity of infection are inversely related, while no such relationship occurs for pheasants or, if it does, it is not as pronounced as for partridges. This approach cannot prove the above hypothesis, but the absence of an inverse relationship between worm intensity and grey partridge body condition would refute the hypothesis and would preclude the need for any further investigation.

Materials and methods

During July–September 1997, 15 individuals of each host species were reared from day-old chicks on sterilised concrete to ensure that no individuals were exposed to nematodes prior to the trial. At 12 weeks of age, up to which no chick mortality had occurred, three individuals of each species were culled to confirm that the birds were free of nematode infection. The remaining birds were sexed, wing-tagged, and weighed to the nearest 5 g. Three individuals of each species were then placed into each of four grass pens (measuring 1.8×3.6 m) located on the rearing field of a gamebird estate in Stirlingshire, Scotland. Previous sampling had confirmed that the rearing field was heavily contaminated with *H. gallinarum* eggs, in which the protozoan *H. meleagridis* was absent. After 40 days, during which the birds were supplied with water, grit and food (gamebird maintenance pellets) ad libitum, all birds were culled and the intensity of *H. gallinarum* infection and host body condition measured.

All worms were removed from the gut of each bird by washing the intestinal and caecal contents through a coarse sieve (1.4 mm) to remove host tissue, and then a fine sieve (0.2 mm) to collect the worms. Sieving is a standard method for collecting gastrointestinal worms (Doster and Goater 1997). The trachea of each host was also examined for nematode parasites. Worms recovered were identified and counted under $\times 25$ magnification of a binocular microscope. The body length of all *H. gallinarum* worms recovered was measured, using an ocular micrometer under $\times 40$ magnification, to the nearest 0.025 mm.

Host body condition was estimated by measuring the pectoralis muscle mass of each bird to the nearest 0.01 g. Lean wet breast muscle mass is highly correlated with the total protein content of gamebirds and, when adjusted for body size, is a good index of condition (Brittas and Marström 1982). Body size was estimated from the length of the left tarsus of each bird, measured to the nearest 0.1 mm. Adjustments were made separately for each host species by fitting a least-squares linear regression to the muscle mass and tarsal length measurements, and adding the residual value generated for each individual to the muscle mass value for a bird of mean body size, as predicted by the fitted equation. This final step provided 'real' values, rather than deviation units, for later illustration.

All analyses were conducted using generalized linear models (GLMs) with both host sex and pen number included as factors, thus controlling for host sex and avoiding pseudoreplication problems. While measurements of worm size and host body condition were analysed using standard GLMs with normal error distributions (Crawley 1993), parasite intensity was analysed using a GLM with an explicitly defined negative binomial error distribution (Wilson et al. 1996; Wilson and Grenfell 1997). This allowed a valid model to be fitted to the aggregated parasite intensity data (see Fig. 1). All analyses were conducted by first fitting the full model, and then discarding the non-significant interaction terms.

Results

Although the majority of nematodes recovered from the experimental birds were indeed the caecal worm *H. gallinarum* (see below), the birds were also infected by

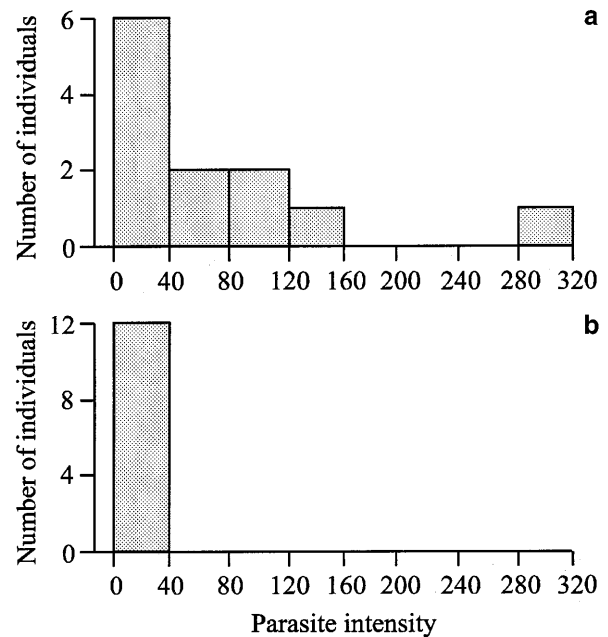


Fig. 1 Frequency distribution of *Heterakis gallinarum* intensity in (a) pheasants ($n = 12$ birds) and (b) grey partridges ($n = 12$ birds), after 40 days exposure to ground contaminated with *H. gallinarum* eggs. 100% of the pheasants were infected with a mean \pm SD of 72.17 ± 83.05 worms, while 92% of the partridges were infected with 5.45 ± 4.27 worms

two other nematode species. An intestinal worm, *Capillaria annulata*, was recovered from 58.33% of the pheasants (with a mean \pm SD of 4.86 ± 5.96 worms per infected bird) and 83.33% of the partridges (with 3.30 ± 2.50 worms per infected bird). A tracheal worm, *Syngamus trachea*, was recovered from 41.67% of the pheasants (with 5.60 ± 4.28 worms per infected bird).

After the 40-day exposure period, the pheasants were infected with more *H. gallinarum* worms than were the partridges (Fig. 1; deviance = 23.37, $df = 1,17$, $P < 0.001$). While there were no significant differences in *H. gallinarum* intensity either among pens (deviance = 7.47, $df = 3,17$, $P = 0.06$) or between sexes (deviance = 3.33, $df = 1,17$, $P = 0.07$), there was a significant interaction between host sex and host species (deviance = 4.81, $df = 1,17$, $P = 0.03$) – parasite intensity differed between the sexes in pheasants (100% of males infected with 85.40 ± 85.22 worms versus 100% of females infected with 6.00 ± 1.41 worms), but not in partridges (100% of males infected with 5.20 ± 2.77 worms versus 86% of females infected with 5.67 ± 5.50 worms).

H. gallinarum worms recovered from pheasants were significantly longer than those recovered from partridges (Fig. 2; $F_{1,17} = 7.79$, $P = 0.01$). There were no differences in worm length either among pens ($F_{3,17} = 1.45$, $P = 0.26$) or between host sexes ($F_{1,17} = 0.12$, $P = 0.73$).

There was no relationship between log-transformed *H. gallinarum* intensity, after the 40-day exposure period, and either pheasant body mass prior to the infection

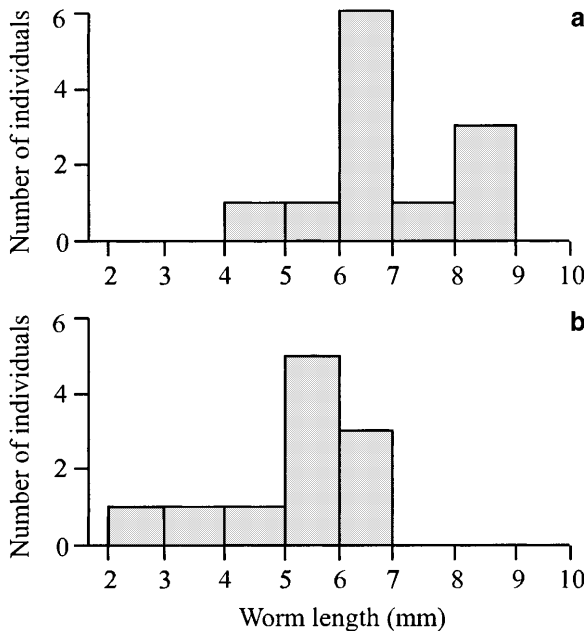


Fig. 2 Frequency distribution of mean *H. gallinarum* body length recovered from (a) pheasants ($n = 12$ birds) and (b) grey partridges ($n = 11$ birds) (one partridge was free of infection). Worms recovered from pheasants had a mean \pm SD length of 7.01 ± 1.25 , while those recovered from partridges had a mean length of 5.18 ± 1.41

trial (Fig. 3a; $F_{1,6} = 0.22$, $P = 0.66$) or pheasant body condition after the trial (Fig. 3b; $F_{1,6} = 0.33$, $P = 0.59$). However, while log-transformed *H. gallinarum* intensity was also unrelated to partridge body mass prior to the infection trial (Fig. 4a; $F_{1,6} = 0.36$, $P = 0.57$), it was negatively correlated with partridge body condition after the trial (Fig. 4b; $F_{1,6} = 6.30$, $P = 0.05$). No sex differences were found in either pheasant ($F_{1,6} = 1.71$, $P = 0.24$) or partridge ($F_{1,6} = 0.57$, $P = 0.48$) body mass prior to the infection trial, or pheasant ($F_{1,6} = 0.06$, $P = 0.82$) or partridge ($F_{1,6} = 0.87$, $P = 0.39$) relative body condition after the trial. Likewise, there were no differences among pens for either pheasant ($F_{3,6} = 3.47$, $P = 0.09$) or partridge ($F_{3,6} = 0.56$, $P = 0.66$) body mass prior to the infection trial, or pheasant ($F_{3,6} = 0.55$, $P = 0.67$) or partridge ($F_{3,6} = 2.14$, $P = 0.20$) relative body condition after the trial.

Discussion

This study investigated the hypothesis that the spread of parasites from released pheasants may have contributed to the decline in wild grey partridge populations. Following controlled exposure, we found that infection by the caecal worm *H. gallinarum* was negatively correlated with grey partridge body condition (Fig. 4b), while being unrelated to pheasant body condition (Fig. 3b). That there was no relationship between the intensity of *H. gallinarum* infection after the 40-day exposure period

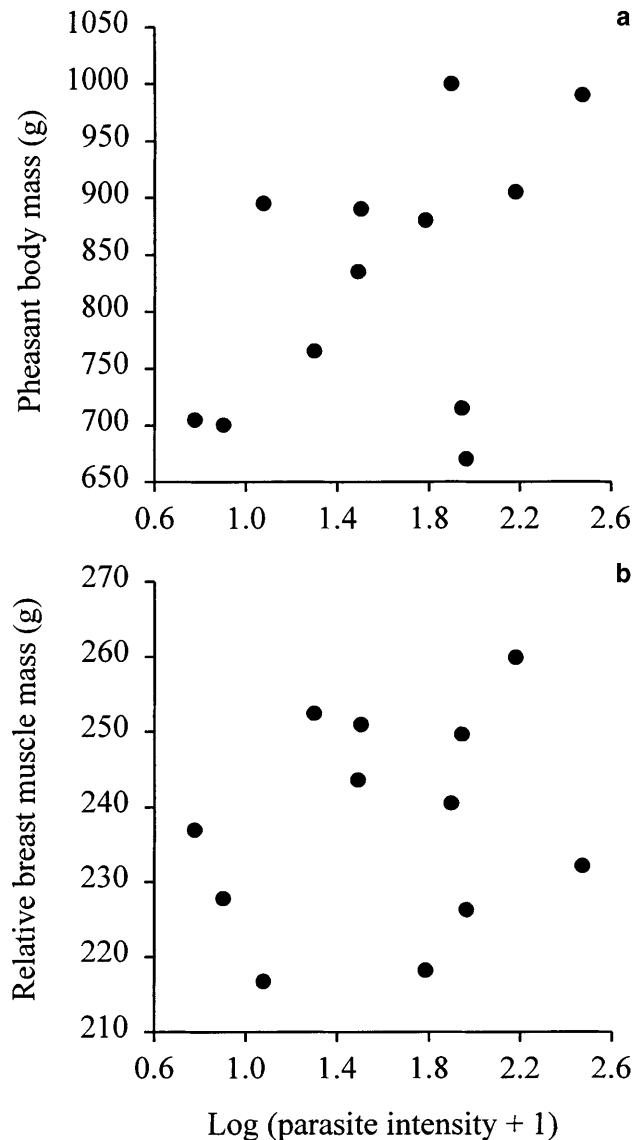


Fig. 3 Relationship between log-transformed *H. gallinarum* intensity and (a) pheasant body mass prior to the infection trial, and (b) lean wet breast muscle mass of pheasants, adjusted for body size, after the trial ($n = 12$ birds). Muscle mass was adjusted to a mean tarsal length of 83.6 mm, using residuals from the regression equation $M = 4.33T - 123.97$ [where M = breast muscle mass (g) and T = tarsal length (mm)]

and partridge body mass prior to the infection trial (Fig. 4a) implies that infection caused the decrease in body condition, and not vice versa. This differential impact does not allow us to refute the hypothesis that parasite-mediated competition between pheasants and grey partridges can adversely affect partridge populations. However, further information concerning parasite transmission both within and between host species, parasite survival and fecundity in the two different hosts, and whether the effect on partridge body condition translates into an effect on host survival and fecundity is required before this hypothesis can be accepted. There is also some evidence to suggest further complications:

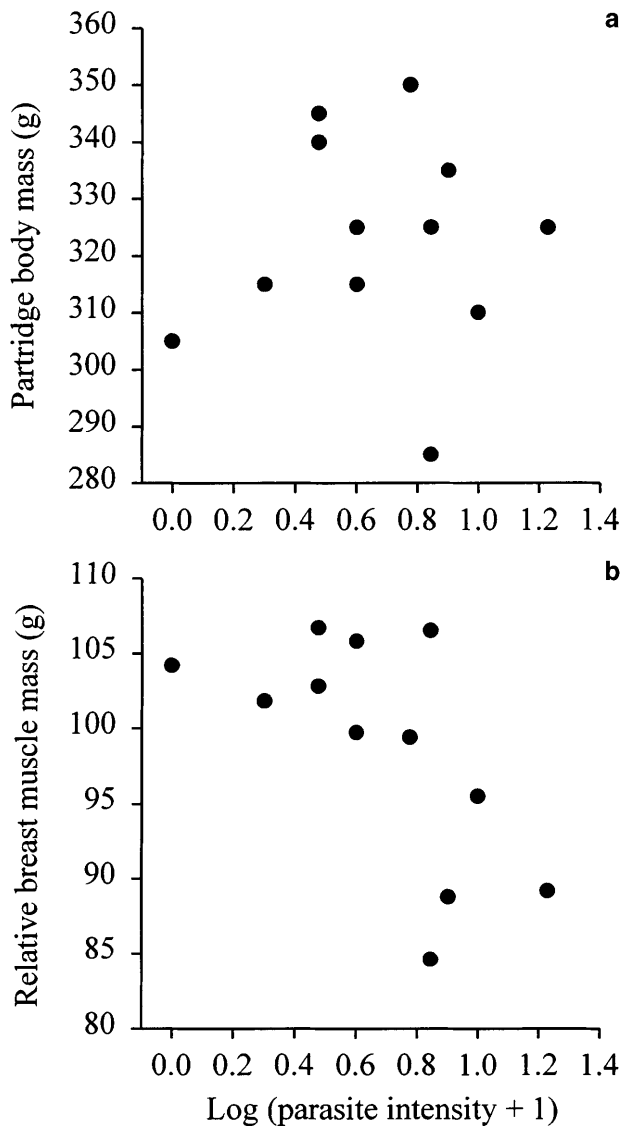


Fig. 4 Relationship between log-transformed *H. gallinarum* intensity and (a) grey partridge body mass prior to the infection trial, and (b) lean wet breast muscle mass of partridges, adjusted for body size, after the trial ($n = 12$ birds). Muscle mass was adjusted to a mean tarsal length of 52.72 mm, using residuals from the regression equation $M = 4.26T - 126.01$ [where M = breast muscle mass (g) and T = tarsal length (mm)]

H. gallinarum may interact with nutritional status in its impact on host fitness (Clapham 1934; R.A.H. Draycott, personal communication), and the presence of the protozoon *H. meleagridis* in *H. gallinarum* eggs may exacerbate the differential impact on pheasants and partridges (Lund and Chute 1971, 1972a).

Some information concerning the survival and fecundity of *H. gallinarum* in pheasants versus grey partridges can be discerned from this limited study. Since the *H. gallinarum* worms recovered from the grey partridges after the 40-day exposure period were significantly smaller than those recovered from the pheasants (Fig. 2), and *H. gallinarum* fecundity is correlated with worm size (Tompkins and Hudson, in press), the

fecundity of worms infecting partridges appears to be less than that of worms infecting pheasants. This difference in host suitability is also the most likely explanation for the lower intensity of *H. gallinarum* infection in the grey partridge, following the 40-day exposure period (Fig. 1), than in the pheasant. Indeed, previous work by Lund and Chute (1972b) has documented both lower survival and lower fecundity of *H. gallinarum* in the grey partridge than in the pheasant. This suggests that the bulk of nematode infection to wild grey partridges in the UK is sourced from reared pheasants, and not from the partridges themselves.

The higher intensity of *H. gallinarum* infection in male than in female pheasants, as seen in this study, has also been documented previously (Hillgarth et al. 1990; Tompkins and Hudson, in press). Hillgarth et al. (1990) suggested that the higher intensities in males may be due to the suppression of the immune system in stressed birds competing for mates. However, since we documented the same pattern, prior to any breeding involvement, this appears to be unlikely. An alternative explanation is that the rate of *H. gallinarum* transmission to male pheasants may be greater than that to female pheasants, possibly due to differences in foraging strategy. Either way, these studies imply that male pheasants are the major source of *H. gallinarum* infection.

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References

- Brittas R, Marcström V (1982) Studies in willow grouse *Lagopus lagopus* of some possible measures of condition in birds. *Ornis Fenn* 59:157–169
- Clapham PA (1934) Some observations on the effect of dietary deficiency on infestation of chickens with the nematode *Heterakis gallinae*. *J Helminthol* 12:123–126
- Clapham PA (1935) Some helminth parasites from partridges and other English birds. *J Helminthol* 13:139–148
- Crawley MJ (1993) *GLIM for ecologists*. Blackwell, Oxford
- Doster GL, Goater CP (1997) Collection and quantification of avian helminths and protozoa. In: Clayton DH, Moore J (eds) *Host-parasite evolution – general principles and avian models*. Oxford University Press, Oxford, pp 396–418
- Hillgarth N (1990) Parasites and sexual selection in pheasants. DPhil. thesis, University of Oxford
- Hillgarth N, Robertson P, Woodburn M (1990) A preliminary survey of pheasant parasites in the wild. Game Conservancy Trust, Fordingbridge
- Holt RD, Lawton JH (1994) The ecological consequences of shared natural enemies. *Annu Rev Ecol Syst* 25:495–520
- Hudson PJ, Greenman J (1998) Competition mediated by parasites: biological and theoretical progress. *Trends Ecol Evol* 13:387–390
- Kanshik RK, Deorani VPS (1969) Effects of experimental infection with *Heterakis gallinarum*. *J Helminthol* 43:69–78
- Keymer IF, Rose JH, Beesley WN, Davies SFM (1962) A survey and review of parasitic diseases of wild and game birds in Great Britain. *Vet Rec* 74:887–894

- Kimmel RO (1988) Potential impacts of ring-necked pheasants on other gamebirds. In: Hallett DL, Edwards WR, Burger GV (eds) Pheasants: symptoms of wildlife problems on agricultural lands. North Central Section of the Wildlife Society, Bloomington, pp 253–265
- Lund EE, Chute AM (1971) Histomoniasis in the chukar partridge. *J Wildl Manage* 35:307–315
- Lund EE, Chute AM (1972a) The ring-necked pheasant (*Phasianus colchicus torquatus*) as a host for *Heterakis gallinarum* and *Histomonas meleagridis*. *Am Midl Nat* 87:1–7
- Lund EE, Chute AM (1972b) Reciprocal responses of eight species of galliform birds and three parasites: *Heterakis gallinarum*, *Histomonas meleagridis*, and *Parahistomonas wenrichi*. *J Parasitol* 58:940–945
- Potts GR (1986) The partridge: pesticides, predation and conservation. Collins, London
- Potts GR, Aebischer NJ (1994) Population dynamics of the grey partridge *Perdix perdix* 1793–1993: monitoring, modelling and management. *Ibis* 137:S29–S37
- Rands MRW (1985) Pesticide use on cereals and the survival of grey partridge chicks: a field experiment. *J Appl Ecol* 22:49–54
- Robertson PA (1996) Naturalised introduced gamebirds in Britain. In: Holmes JS, Simons JR (eds) The introduction and naturalisation of birds. HMSO, London, pp 63–69
- Ruff MD, McDougald LR, Hansen MF (1970) Isolation of *Histomonas meleagridis* from embryonated eggs of *Heterakis gallinarum*. *J Protozool* 17:10–11
- Sotherton NW (1998) Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biol Conserv* 83:259–268
- Southwood TRE, Cross DJ (1969) The ecology of the partridge. III. Breeding success and the abundance of insects in natural habitats. *J Anim Ecol* 38:497–509
- Tapper S (1992) Game heritage: an ecological review from shooting and gamekeeping records. Game Conservancy Trust, Fordingbridge
- Tompkins DM, Hudson PJ (in press) Regulation of nematode fecundity in the ring-necked pheasant (*Phasianus colchicus*): not just density dependence. *Parasitology*
- Wilson K, Grenfell BT (1997) Generalized linear modelling for parasitologists. *Parasitol Today* 13:33–38
- Wilson K, Grenfell BT, Shaw DJ (1996) Analysis of aggregated parasite distributions: a comparison of methods. *Funct Ecol* 10:592–601
- Wright VL, Farris AL, Graham DL, Fielder WR (1980) Effects of *Heterakis* and *Histomonas* on the survival of juvenile gray partridge. In: Peterson SR, Nelson L (eds) Proceedings of Perdix II gray partridge workshop. University of Idaho, Moscow, pp 156–164