

Can parasites synchronise the population fluctuations of sympatric tetraonids? – examining some minimum conditions

Per R. Holmstad, Peter J. Hudson, Vigdis Vandvik and Arne Skorping

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Sympatric populations of tetraonid birds tend to fluctuate in synchrony, at least on local scales. If shared parasites among sympatric populations of different tetraonid species are to operate as a local, synchronizing factor for population fluctuations at least two conditions should be met: i) the host species should share the same (or similar) parasite species, and ii) geographical location should contribute significantly more to the variation in the parasite species composition and abundance than differences among host species. We examined these conditions among subpopulations of sympatric willow ptarmigan and rock ptarmigan and found that host species shared a common pool of parasite species, and geographic location was more important than host species in determining parasite abundance across locations. There was no time lag between density oscillations in the two hosts, suggesting a symmetrical pattern of transmission and maintenance of parasites within habitats governed by the density of hosts and the environment. These findings are consistent with the idea that parasites may play a role in generating synchronous density fluctuations, but large scale experiments are needed to verify this hypothesis.

P. R. Holmstad, V. Vandvik and A. Skorping, Dept. of Biology, Univ. of Bergen, Realflågbygget, Allégaten 41, NO-5007 Bergen, Norway (per.holmstad@zoo.uib.no). – P. J. Hudson, Biology Dept, Mueller Lab, Penn State Univ., PA 16802 USA.

Populations of small rodents and tetraonid birds are characterized by their tendency to exhibit regular fluctuations in abundance. Such population cycles are not species-specific (Moss and Watson 2001), as cycle periods may show profound geographical variation within species (Hudson 1992, Lindström 1994), and there is evidence that sympatric populations of different species will tend to fluctuate in synchrony (Lindén 1989, Small et al. 1993, Lindström et al. 1996, Cattadori et al. 2000).

At finer spatial scales, the degree of synchrony between subpopulations often depends on the scale of observation (Hudson 1992, Moss et al. 1996, Cattadori et al. 1999, Moss et al. 2000). A general pattern observed for many species is a declining synchrony with increasing distance between populations (Hudson 1992, Ranta

et al. 1995a, b, Lindström et al. 1996, Cattadori et al. 1999, 2000). This pattern, coupled with modelling and analyses of comparative data, tends to support the Moran hypothesis (Moran 1953, Royama 1992). This may also explain why the periodicity of tetraonid cycles seems to be a characteristic of locations more than of species, as related species with similar density-dependent structures probably would be influenced by the same set of regulatory processes and show a correlated response to the environment (Cattadori et al. 2000, Moss and Watson 2001). Local synchrony between subpopulations may arise if the different species were regulated by the same or similar food plants (Hörnfeldt et al. 1986), provided that this generated a similar density-dependent structure and the plants suffered from similar environmental conditions. Trophic interactions could cause

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synchrony in a range of secondary prey populations when generalist predators switch from one prey type (usually microtines) to alternative prey like grouse species (Hagen 1952, Steen et al. 1988, Small et al. 1993, Kjellander and Nordström 2003). Specialist natural enemies like parasites could also act to generate synchronized population fluctuations if their free-living stages suffer from common environmental conditions. Either way, cycles should be driven by similar mechanisms acting on the population within specific locations rather than by broad species-specific factors.

Any hypothesis concerning the cause of instability in population densities needs to be tested experimentally at the correct scale by direct manipulation of the mechanism (Hudson and Bjørnstad 2003). To date, the only mechanism that has been tested experimentally at the population scale with replication, is the hypothesis that parasite-induced reduction in fecundity is the principal factor destabilising host dynamics. Hudson et al. (1998) showed that application of anthelmintics prevented expected density declines and reduced variance in red grouse populations both within and between populations. In this paper we examine the hypothesis that shared parasites among sympatric populations of different host species may operate as a local synchronising factor for host population densities. The 'parasite hypothesis' can only be a feasible explanation for locally synchronized population cycles among different hosts species if; i) host species share either the same or similar parasite species, and ii) geographical location contribute significantly more to the variation in the parasite species composition and abundance than differences among host species. We tested these conditions using data from a field study of subpopulations of sympatric willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. mutus*) at seven locations along a coast-inland gradient in northern Norway.

Material and methods

A total of 159 willow ptarmigan and 129 rock ptarmigan were collected from seven different areas in Troms County, northern Norway, during September 1992 (Holstad et al. 1994). These locations represent a stratified subsampling of habitats along a gradient from continental inland locations (area 1 and 2), via intermediate fjord localities (area 4, 5 and 6) to more exposed coastal localities on islands off the Norwegian coast (area 7 and 8). In each area willow and rock ptarmigan were collected from overlapping populations at sites where both species could be harvested during a days hunt. Altitude at which each bird was shot was recorded. All birds were collected and examined for endoparasites following procedures given in Holmstad and Skorping (1998) and Holmstad et al. (2003).

Hunting statistics have been shown to be a good proxy of population abundance (Cattadori et al. 2003). Hunting records were available for three of our populations; area 2, 5 and 7, in addition to Statskog Troms (mainly inland areas). None of the hunting records could be corrected for hunting effort. Line transect counts of willow ptarmigan were available from area 1 (1980–2003) and area 7 (1990–2003). Each transect was 150 m wide and the total transect length in area 1 was 23 km and in area 7 716.6 km. Counting was undertaken in late August by two to three observers that used trained pointing dogs to locate and flush birds. Care was taken to avoid counting birds more than once. Hunting bags and line transect counts from the same or different areas were regarded as relative, independent measures of ptarmigan densities reflecting trends in population fluctuations that could be tested against each other to check for synchrony among host subpopulations. Host population growth rates were calculated based on annual hunting records or August counts as $\ln(t/t-1)$. Hunting statistics and transect counts were standardized to mean = 0 and SD = 1 (standard score = (raw score - mean)/SD) in order to take account of relative variations between populations.

The overall responses of the parasite community within individual birds to host species, geographic location, and to the mass, age, and sex of the individual hosts were quantified using ordinations in the CANOCO[®] statistical software. First, a detrended correspondence analysis (DCA; Hill and Gauch 1980), with detrending-by-segments and non-linear rescaling of axes, was used to determine the length of the gradients in the parasite dataset. Linear methods were chosen, and the compositional responses to the explanatory variables were quantified by partial principal components analysis (pPCAs) and standardised partial redundancy analyses (pRDAs) (ter Braak 1994, Jongman et al. 1995). Statistical significances of these responses were tested by Monte Carlo permutation tests (ter Braak 1990) for all canonical axes using 499 unrestricted permutations. Parasite counts were $\ln(x+1)$ transformed, and the ordinations were standardised by species abundance to remove the effect of differences in maximum intensities (total parasite counts) among species. As blood samples were not collected in all areas (Table 1), blood parasites were made passive in the analyses. However, analysis of the data from the four areas where all parasites were collected indicated that these parasites did not deviate from the general community pattern. Ordinations were performed in CANOCO 4.5 (ter Braak and Šmilauer 2002).

Results

Within each of the two areas where hunting records were available for both willow and rock ptarmigan, both

hunting records of the two host species (Fig. 1) and their population growth rates were well correlated (Statskog Troms; $r=0.66$, $N=16$, $p=0.005$, and area 7; $r=0.59$, $N=12$, $p=0.04$), indicating that these populations fluctuated in synchrony. At larger geographical scales, the synchrony disappeared, as neither hunting records (Fig. 1) nor host population growth rates (willow ptarmigan; $r=-0.03$, $N=11$, $p=0.93$, and rock ptarmigan; $r=0.16$, $N=11$, $p=0.64$) were correlated within hosts between the areas Statskog Troms and area 7.

In area 7, line-transect counts of willow ptarmigan were correlated with hunting records for both willow ($r=0.77$, $N=13$, $p=0.002$) and rock ($r=0.78$, $N=13$, $p=0.002$) ptarmigan. Total hunting records of willow and rock ptarmigan were correlated between the coastal locality area 7 and the fjord island area 5 (Fig. 2A). At inland localities, willow ptarmigan hunting records in area 2 and line transect counts in area 1 were correlated (Fig. 2B). There were no significant correlations between any combinations of data across larger spatial scales (coast vs inland or inland vs fjord) suggesting that synchrony disappeared as distance among sites increased.

Recorded altitudes for each bird shot were standardized (mean = 0 and SD = 1) within each area and then pooled into a single variable. Rock ptarmigan was consistently shot at higher elevations than willow ptarmigan across all areas indicating that there was a spatial segregation with little overlap between the two host species in September (Mann–Whitney U-test; $Z_{adj} = -12.5$, $N=244$, $p < 0.0001$).

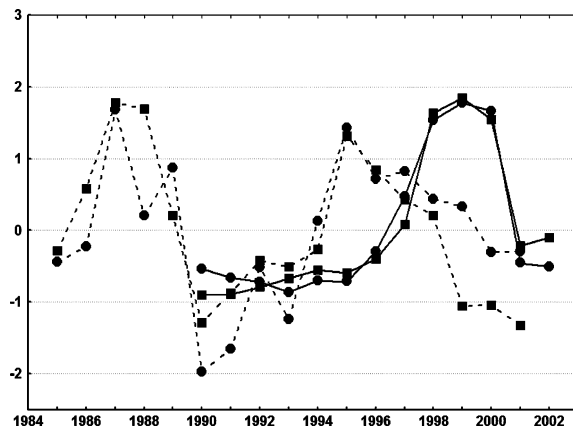


Fig. 1. Standardized hunting records (mean = 0, SD = 1) of willow and rock ptarmigan from two areas in Troms County, northern Norway, area 7; willow ptarmigan (■, solid line) and rock ptarmigan (●, solid line), Statskog Troms; willow ptarmigan (■, broken line) and rock ptarmigan (●, broken line). Bag records for the two host species were significantly correlated within each area in both Statskog Troms ($r=0.72$, $N=17$, $p=0.001$) and in area 7 ($r=0.97$, $N=13$, $p < 0.0001$), but standardized numbers shot of each species were not correlated between areas neither for willow ptarmigan ($r=-0.12$, $N=12$, $p=0.70$) nor rock ptarmigan ($r=0.31$, $N=12$, $p=0.33$).

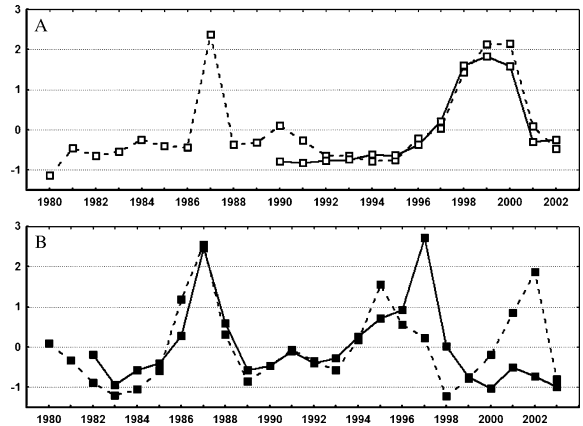


Fig. 2. (A): Standardized (mean = 0 and SD = 1) total hunting records including both willow ptarmigan and rock ptarmigan from the coastal area 7 (□, solid line) and the fjord location area 5 (□, broken line); hunting records were correlated between these two island areas ($r=0.94$, $N=13$, $p < 0.0001$). (B): Standardized line transect counts of willow ptarmigan in area 1 (■, broken line) plotted together with standardized hunting records of willow ptarmigan from area 2 (■, solid line); the line transect counts and bag records of these two inland areas were correlated ($r=0.55$, $N=22$, $p=0.008$).

Eleven parasite taxa were identified in the ptarmigans, nine of these occurred in both hosts, while two rare blood parasites, *Trypanosoma avium* and *Atoxoplasma* sp., were only recorded in willow ptarmigan (Table 1). Willow ptarmigan had significantly higher prevalences of all parasite species than rock ptarmigan (Wilcoxon Matched pairs test; $Z=2.13$, $N=11$, $p=0.03$), indicating that there were species-related differences in the frequency of infections.

Geography was by far the best explanatory variable for parasite abundance, with site (i.e. sampling location) accounting for 18% of the variability. This among-site variability was to a large extent structured along the coast-to-inland gradient, as area (i.e. sites nested under coast, fjord and inland) explained 11.9% of the variability in parasite composition (Table 2). In contrast, species-related differences were reflected as a significant difference in parasite composition between willow and rock ptarmigan in the multivariate analysis, but this difference only explained 3% of the variability in parasite community composition among all host individuals in the study (Table 2). Thus, geographical location contributed significantly more to the variation in parasite species composition and abundance than host species. While the largest fraction of the compositional variance (76.1%) was found locally, among birds within populations of each species at each site, this variability appears largely stochastic, as only 3.2% can be accounted for by host characteristics such as gender, age, or body weight (Table 2).

Table 1. Prevalences (percentage of hosts infected) of parasites species in willow ptarmigan (*L. lagopus*) and rock ptarmigan (*L. mutus*) from seven localities in Troms County, northern Norway, 1992. There were two inland localities (area 1 and 2), three fjord localities (area 4, 5 and 6) and two coastal localities (area 7 and 8). Asterisks (*) indicate that blood samples were not collected.

Parasite	Host	Inland		Fjord			Coast	
		Area 1	Area 2	Area 4	Area 5	Area 6	Area 7	Area 8
	<i>L. lagopus</i>	N = 32	N = 24	N = 23	N = 21	N = 2	N = 35	N = 22
	<i>L. mutus</i>	N = 19	N = 30	N = 24	N = 19	N = 10	N = 24	N = 3
<i>Eimeria</i> spp.	<i>L. lagopus</i>	87.5	75.0	76.2	95.2	50.0	67.6	77.3
	<i>L. mutus</i>	84.2	93.3	95.8	100.0	80.0	87.0	100.0
<i>L. lovati</i>	<i>L. lagopus</i>	58.8	71.4	90.5	*	*	54.5	*
	<i>L. mutus</i>	54.5	8.3	66.7	*	*	40.0	*
<i>H. microps</i>	<i>L. lagopus</i>	40.6	33.3	23.8	19.0	100.0	29.4	45.5
	<i>L. mutus</i>	15.8	26.7	20.8	0.0	30.0	13.0	0.0
<i>A. compar</i>	<i>L. lagopus</i>	75.0	75.0	0.0	23.8	0.0	2.9	0.0
	<i>L. mutus</i>	47.4	53.3	0.0	0.0	0.0	0.0	0.0
<i>T. tenuis</i>	<i>L. lagopus</i>	0.0	0.0	4.4	0.0	50.0	51.4	100.0
	<i>L. mutus</i>	0.0	0.0	0.0	0.0	10.0	12.5	66.7
<i>S. papillocerca</i>	<i>L. lagopus</i>	15.6	8.3	9.5	0.0	0.0	15.4	18.2
	<i>L. mutus</i>	21.1	6.7	8.3	5.3	0.0	17.4	0.0
<i>C. caudinflata</i>	<i>L. lagopus</i>	0.0	0.0	4.8	4.8	0.0	32.4	9.1
	<i>L. mutus</i>	15.8	0.0	29.2	5.3	0.0	8.7	0.0
<i>P. urogalli</i>	<i>L. lagopus</i>	0.0	0.0	38.1	4.8	0.0	5.9	0.0
	<i>L. mutus</i>	0.0	0.0	8.3	0.0	0.0	0.0	0.0
<i>Microfilaria</i>	<i>L. lagopus</i>	5.9	0.0	0.0	*	*	9.1	*
	<i>L. mutus</i>	0.0	8.3	0.0	*	*	0.0	*
<i>T. avium</i>	<i>L. lagopus</i>	0.0	0.0	9.5	*	*	0.0	*
	<i>L. mutus</i>	0.0	0.0	0.0	*	*	0.0	*
<i>Atoxoplasma</i> sp.	<i>L. lagopus</i>	0.0	0.0	0.0	*	*	4.5	*
	<i>L. mutus</i>	0.0	0.0	0.0	*	*	0.0	*

Discussion

The aim of this study was to explore whether parasites could play a role in generating synchronous density fluctuations in two sympatric host species. We found that rock ptarmigan and willow ptarmigan showed correlated density and growth rate fluctuations within sites, and between sites in close proximity, but fluctuations in coastal/fjord areas and inland areas were not correlated. Parasites could account for such localised synchrony among two or more sympatric hosts provided that at least two conditions are met. The first condition is that hosts showing synchronous popula-

tion fluctuations should share a common pool of parasites. This condition was met in our study system, as 9 out of 11 species were found in both hosts. The second condition was also met, as geographic location explained more of the variability in parasite abundance than host species did. This implies that parasite abundances were, on average, more similar between individuals of different host species living within the same area than between individuals of the same host species living in different areas. Thus, our findings are consistent with the hypothesis that shared parasites may contribute to synchronize local host population dynamics.

Table 2. Summary of (partial) RDA's and PCA's to investigate the explanatory power of geography and host species (*L. mutus* or *L. lagopus*), as well as the gender, age, and bodymass of the individual hosts on parasite abundance. All p-values are the result of 499 permutations.

Effects	Model		Variance components		
	Variables	Covariables	% Variance	F-ratio	p (499)
Among-population scale					
Sites	S		18.0	9.9	<0.002
Geographic area	A		11.9	18.4	<0.002
Host species	H		3.0	8.5	<0.002
Host effects among areas	H × A	H + A	3.3	5.4	<0.002
Total among-population variability	H × S		23.9		
Within-population scale					
Host age	Y	H × S	2.5	8.9	<0.002
Host bodymass	M	H × S	1.3	4.5	<0.002
Host gender	G	H × S	0.4	1.3	0.298
Total variance accounted for	Y + M + G	H × S	3.2		
Total within-population var.		H × S	76.1		

Our results can not refute the hypothesis that density fluctuations among sympatric ptarmigan were caused by other factors, if parasites were passively following host densities through density-dependent transmission. However, both theoretical and empirical studies suggest that parasites may be the cause of fluctuations in host densities, rather than the other way around (Anderson and May 1978, May and Anderson 1978, Scott 1987, Hudson et al. 1998, Tompkins and Begon 1999). An earlier study on willow ptarmigan in Norway suggested that increased abundance of *Eimeria* spp. was associated with population declines (Brinkmann 1926), and these parasites were the most common in this study occurring in both hosts on all areas. Moreover, in an ongoing long term study within two of the areas reported here, we found that several of the parasites were associated with reduced body mass, decreased breeding success and decreased host population growth rates in willow ptarmigan (P. R. Holmstad, P. J. Hudson and A. Skorping, unpubl.). In that study we also found that the abundance of different parasite species tended to covary within years, indicating that the same local factors affected transmission success of different parasites. Thus, for willow ptarmigan there is some evidence for the idea that parasites may drive fluctuations in host density. Any effect of parasites on host densities is likely to differ in magnitude between host species, but this difference should affect the amplitude of density fluctuations in each of the species, not the synchrony among host subpopulations. The effect of parasites might differ in magnitude between areas due to qualitative and quantitative differences in the abundance of parasites, but this does not affect our conclusions since synchrony tend to decrease with distance between subpopulations in our and other studies (Hudson 1992, Ranta et al. 1995a, b, Lindström et al. 1996, Moss and Watson 2000).

Parasites may drive density fluctuations of sympatric hosts in two general ways. The first is when there is asymmetry between hosts and the primary host forces oscillations in the secondary host by acting as a reservoir for parasites (Greenman and Hudson 1997). The second is when the transmission within and between host species is symmetrical, and parasites drive oscillations in both host species, with local synchronisation resulting from effects of environmental variation on parasite transmission (Greenman and Hudson 1997, 1999a, b). Host species explained very little of the variance in parasite abundances, however, and this does not support the idea of a reservoir host, but rather that the two species sustained parasite communities consisting of several shared species that were transmitted and maintained within and among the host populations. Host species show spatial segregation during the entire breeding season and autumn, and occurrence in mixed flocks are restricted to periods in late autumn or winter (Cramp 1980, Watson et al. 1998, pers obs.). Since species mainly

overlap spatially when prevailing temperatures are below zero and infective stages will not develop, interspecific transmission of parasites is likely to be low. Thus, there might be some interspecific exchange of parasite transmission stages where ptarmigan distributions overlap, but it is unlikely that this is the most important factor shaping the parasite communities within either host population. Additionally, in areas with records of shot willow and rock ptarmigan, density oscillations and host population growth rates of both species were correlated, and fluctuations oscillated in synchrony with no detectable time lag. This is in accordance with Myrberget (1974), who found that chick production in willow and rock ptarmigan was correlated within 71 areas over 10 years time. Directional transmission of parasites from one host species to the other would probably not synchronize fluctuations of sympatric host populations, but rather lead to a systematic delay in the oscillations of the secondary host relative to the source host across sites, where the time lag would depend on the between versus within-species parasite transmission rates. Therefore, transmission of similar parasite species within and between species is more likely to be symmetrical depending on host densities and/or common environmental variation.

In an ongoing long term study of willow ptarmigan parasites conducted in two of the areas reported here, one inland (area 1) and one coastal (area 7) locality, there was considerable temporal variation in both host densities and parasite abundances (P. R. Holmstad, P. J. Hudson and A. Skorping, unpubl.). This suggests that the infection pressure experienced by host populations may differ markedly between years. However, it is likely that between-year differences in host densities or weather conditions would affect parasite communities of both host populations concurrently and in the same direction, since population densities of both hosts are closely correlated and parasite transmission seemed to be symmetrical within areas. Thus, although parasite abundance within areas will differ temporally in sympatric ptarmigan populations, we do not expect that the actual patterns revealed in this study would have looked very different in other years.

A final test of the long term predictions concerning possible parasite-mediated synchronization of population fluctuations would require large-scaled, longitudinal field studies conducted concurrently in several subpopulations of ptarmigan or other tetraonids, involving both untreated control subpopulations and manipulated subpopulations with removal of parasites. Testing our hypothesis experimentally would thus require significant resources, but the results presented here suggest that such an effort might provide valuable contributions to our understanding of the mechanisms involved in generating synchronous density fluctuations among different host species.

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