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Parasite tags in ecological studies of terrestrial hosts: a study on ptarmigan (*Lagopus* spp.) dispersal

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The spatial distributions of parasites may provide valuable information in studies on host ecology. This study was conducted in Troms County, Northern Norway, and focussed on the spatial and temporal variation in abundance of two nematode parasites, *Ascaridia compar* and *Trichostrongylus tenuis*, infecting the gastrointestinal tract of Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*Lagopus mutus*). In an inland area prevalence of *A. compar* varied between 52.2–78.1% in September during 6 years of sampling, and in a coastal area that was sampled for 10 years, the prevalence of *T. tenuis* ranged between 25.0–75.4%. Both nematodes attained significantly higher prevalences in willow ptarmigan than in Rock Ptarmigan. The nematodes showed marked differences in geographical distributions in September, where *A. compar* was common at inland localities while *T. tenuis* only was found in hosts at coastal islands. Practical use of these parasites as biological tags suggested a coast to inland winter dispersal in Rock Ptarmigan, especially among juvenile hens, but no dispersal was recorded in Willow Ptarmigan. The use of biological tags in general and the use of nematodes as indicators of ptarmigan dispersal are discussed.

1. Introduction

Parasite tags can be a useful ecological tool to differentiate between animals originating from different sub-populations, and have been successfully applied in studies of fish stocks to determine their geographical origins, migration routes, spawning and nursery areas (Williams *et al.* 1992, MacKenzie & Abaunza 1998). Parasite tags have some advantages over conventional tags, since the tagging process occurs naturally in the host habitat, thus minimising the potential effects of handling and maintenance stress on animals. Used as a tool in ecological studies, parasite tags may provide a supplement to conventional field methods by reducing the effort needed in capture–tagging–recapture events by providing supporting evidence to observed dispersal patterns. Moreover, a good parasite tag will infect most or all of the host population belonging to a certain geographic area, an efficiency unsurpassed by studies using artificial tags.

Despite the many successful applications on marine hosts like fish, mammals and invertebrates (MacKenzie 1987, 2002), the use of parasites as biological tags in studies of terrestrial animals has received little attention. There should be no reason not to use parasite tags in terrestrial studies, for instance where the geographical origins of dispersing birds are of interest. If a parasite species should be useful in such studies, some criteria have to be fulfilled: 1) There must be a difference in parasite species assemblages between host subpopulations that reflects the patchiness of the host population, 2) Candidate tags have to infect a large proportion of the host subpopulation, 3) The parasite chosen must persist in the subject host long enough to be recorded after dispersal, 4) The parasite should not cause selective mortality of hosts or cause significant changes in host behaviour, and 5) The prevalence of infection should remain relatively constant from year to year (MacKenzie & Abaunza 1998).

Here, we evaluate whether parasite tags could be used in studies of winter dispersal of two game birds, the sympatric Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*Lagopus mutus*). These hosts are infected with a range of different parasites (Sonin & Barus 1981, Holmstad & Skorping 1998). Of these species, two intestinal nematodes show a distinct distribution pattern in Norway; *Ascaridia compar* (Schrank 1790) have been found in drier inland localities (Huus 1928) while findings of *Trichostrongylus tenuis* (Mehlis 1846) have been restricted to islands along the coast (Holstad *et al.* 1994).

The distribution patterns of *A. compar* and *T. tenuis* can be used to evaluate the use of these parasites as tags in a terrestrial environment. As all former studies were cross-sectional, little is known about the temporal dynamics of these nematodes, a point that has received little attention in most studies that have suggested parasite species as biological tags (MacKenzie & Abaunza 1998, but see Margolis 1998).

In this study we sampled subpopulations of Willow and Rock Ptarmigan along a coast–inland gradient, and checked them for the parasites *A. compar* and *T. tenuis*. Our objectives were: *i*) to confirm that regional differences in the distribution of *A. compar* and *T. tenuis* occur between subpopulations of Willow and Rock Ptarmigan in autumn, *ii*) to evaluate if any of these nematode species could be used as biological tags with special emphasis on the long-term variability of the proposed parasite tags, and *iii*) to use the proposed tags to investigate whether Willow Ptarmigan or Rock Ptarmigan dispersed along a coast–inland gradient in winter, and if present, determine whether such dispersal was sex or age biased.

2. Material and methods

2.1. Winter dispersal in *Lagopus* spp.

The empirical evidence for winter dispersal in Willow and Rock Ptarmigan is conflicting, although anecdotal information is abundant among hunters (Steen 1989). Conventional marking and radio-tracking of Fennoscandian Willow Ptarmigan have revealed mainly small-scale dispersal in the range of 0.5–2 km for adult birds and 2–6 km in juveniles (Myrberget 1976, Pedersen *et al.* 1983, Smith 1997), although some individuals have been recaptured as far as 750 km from the place of tagging (Myrberget 1976). In Alaska, regular seasonal migrations of Willow Ptarmigan occurred between coast and inland in some areas (Irwing *et al.* 1967), whereas in others more short-range movements were recorded (Gruys 1993). Winter movements or migrations over larger distances have been reported in Russia (Dementiev & Gladkov 1952). Very little is known about Rock Ptarmigan dispersal in Fennoscandia. In Iceland, analysis of the grit of Rock Ptarmigan in winter confirmed dispersal from Greenland (Gudmundsson 1972). Studies using conventional tags have shown that ringed or banded Rock Ptarmigan may move over large areas in winter in Iceland and Svalbard (Gudmundsson 1960, Unander & Steen 1985, Gardarsson 1988).

In most avian species, dispersal seems to be greater in females than in males (Greenwood 1980). In Iceland female Rock Ptarmigan, and then especially juveniles, were more likely to disperse over longer distances than males (Gardarsson 1988). Dispersal of Willow Ptarmigan also seemed to be age and sex biased, and again, juvenile hens have shown the longest dispersal distances (Irwing *et al.* 1967, Myrberget 1976, Smith 1997). As dispersal occurs in late autumn and winter for Willow Ptarmigan (Irwing *et al.* 1967, Myrberget 1976, Smith 1997) and Rock Ptarmigan (Unander & Steen 1985, Gardarsson 1988), transmission of parasites is likely to be very low, because of snow that will cover eggs or larvae and prevailing temperatures below zero which will halt or delay development of transmission stages (Soulsby 1982). The parasites observed during winter should therefore reliably reflect transmission that occurred in the hosts' summer or autumn ranges. Considering the longevity of these parasites, infections of *A. compar* have been found during winter (Wissler & Halvorsen 1977), and infected hosts have also been found in spring (Brinkmann 1923, Huus 1928). Infections of *T. tenuis* have survived for over two years in captive Red Grouse (*Lagopus lagopus scoticus*), with little mortality (Shaw & Moss 1989). Thus, both candidate tag species have an adequate cross-seasonal life span to detect dispersal during winter and early spring.

2.2. Collection of birds and lab procedures

Willow and Rock Ptarmigan are sympatric species living in a strongly seasonal environment, where transmission of different parasites follows a seasonal pattern (Huus 1928, Wissler & Halvorsen 1977). To minimise the effect of season, 118 of the Willow Ptarmigan used in this study were shot in the period 10–20 September 1992 (median sampling day was 12 September), and 95 of the Rock Ptarmigans were shot in the period 10–30 September 1992 (median sampling day was 14 September) from six different areas in Troms county, Northern Norway (see Holstad *et al.* 1994 for details on sampling locations). However, the 33 Willow Ptarmigan and 24 Rock Ptarmigan from Area 7 had to be collected later due to local hunting regulations, between 17. September and 13. October 1992 (median sampling day was 20. September).

The six areas represent a stratified subsampling of habitats along a gradient from continental inland locations (Area 1 and 2), via intermediate fjord localities (Area 4 and 5) to more exposed coastal localities on islands off the Norwegian coast (Area 7 and 8). The Norwegian Meteorological Institute supplied data on mean summer temperatures and annual rainfall for the station at Frihetsli which is located 10 km southeast of Area 1 at 228 meters above sea level, and the city of Tromsø, where the meteorological station is located 100 meters above sea level 20 km east of Area 7. The most notable feature of this inland-coast gradient is the difference in annual precipitation (30 years running mean of annual precipitation; Frihetsli = 282 mm and Tromsø = 1031 mm), but summer temperatures (30 years running mean for June, July and August) were only slightly different between Frihetsli and Tromsø (11.3°C and 10.6°C, respectively).

In an ongoing study on the temporal variability of ptarmigan parasites, the Willow Ptarmigan subpopulation in one of the coastal areas (Area 7) have been sampled annually in September from 1993 to 2002, which gives 577 additional host records for that area. We also collected a total of 190 Willow Ptarmigan from Area 1 during September 1995 and from 1998 to 2003. From these longitudinal studies, data on infections of *T. tenuis* and *A. compar* will be used to evaluate the stability of the proposed tags. Small samples of Willow Ptarmigan from Area 2 and 8 were also collected during September 1999 and 2000.

We also collected a total of 239 Willow Ptarmigan and 317 Rock Ptarmigan from inland and coastal areas in Troms County, Northern Norway, towards the end of the hunting season between 20 January and 15 March in 2000 and 2001. Hunters mainly delivered complete birds that could be sexed, but in some cases we obtained intestines or the intestines together with one of the wings for age determination. The birds were frozen at minus 20 °C, and later thawed at room temperature for laboratory analysis. Birds were sexed by examination of the gonads. The small intestine was cut open and visually examined for *A. compar*. Isolating and counting *T. tenuis* was done by cutting open the caecal walls, which were scraped and washed together with the lumenal contents in a sieve with a mesh width of 75 μm. The filtrate was then examined in a counting chamber using a stereo microscope at 10× magnification to count and collect helminths.

The overall responses of the intensities of *A. compar* and *T. tenuis* to sites or sites nested under geographic region (inland, fjord, coast) and host species, age and sex were quantified and tested using standardised (partial) redundancy analyses ((p)RDAs) (ter Braak 1994, Jongman *et al.* 1995). Parasite counts were ln(x+1) transformed, and the ordinations were run on a correlation matrix (i.e. standardised by parasite species abundance) to remove the effect of differences in maximum intensities among parasite species.

The effects were tested statistically by Monte Carlo permutation tests (ter Braak 1990) for all canonical axes using 999 unrestricted permutations under the reduced model. Ordinations were performed in CANOCO 4.5, and a diagram including centroids was drawn in CANODRAW 4.0 (ter Braak & Šmilauer 2002).

3. Results

The two species of nematodes; *A. compar* and *T. tenuis*, showed a marked difference in spatial distribution in both host species (Table 1a, b). A considerable fraction, 62.0%, of the variation in the intensities of *A. compar* and *T. tenuis* was explained by sites nested under the geographic regions coast, fjord or inland (F = 96.3, P(999) = 0.001). Individual sampling sites, when regions were controlled for, only explained a further 4.8% (F = 4.2, P(999) = 0.02) of the total variance in parasite intensities. While there were also significant differences in infections of *A. compar* and *T. tenuis* among the host species, this factor explained only 3.5% of the variance (F = 4.3, P(999)= 0.03). The spatial heterogeneities in the distributions of *T. tenuis* and *A. compar* together with effects of host species on nematode infections are plotted in Fig. 1. Host age and sex had little impact on parasite infections (F = 2.1, P(999) = 0.135, and F = 0.6, P(999) = 0.50, respectively).

Both prevalence (Area 1: $\chi^2 = 9.57$, P = 0.002,

Table 1.Prevalence (Pr), mean intensity (MI) and range (R) of *Ascaridia compar* and *Trichostrongylus tenuis* in a) 151 Willow Ptarmigan (*L. lagopus*), and b) 119 Rock Ptarmigan (*L. mutus*) collected from six areas in Troms County, 1992.

a) Willow Ptarmigan

	Area code	1	2	4	5	7	8
	n	24	31	21	21	33	21
A. compar	Pr	75.0	74.2	0	23.8	3.0	0
	MI	6.1	13.3	–	1.2	1.0	–
	R	1–22	1–97	–	1–2	1	–
T. tenuis	Pr	0	0	4.8	0	54.5	100
	MI	–	–	7.0	–	68.4	67.1
	R	–	–	7	–	1–560	4–151

b) Rock Ptarmigan

	Area code	1	2	4	5	7	8
	n	30	19	19	24	24	3
A. compar	Pr	53.3	47.4	0	0	0	0
	MI	2.8	4.7	–	–	–	–
	R	1–8	1–18	–	–	–	–
T. tenuis	Pr	0	0	0	0	12.5	66.7
	MI	–	–	–	–	1.7	38.5
	R	–	–	–	–	1–2	12–65

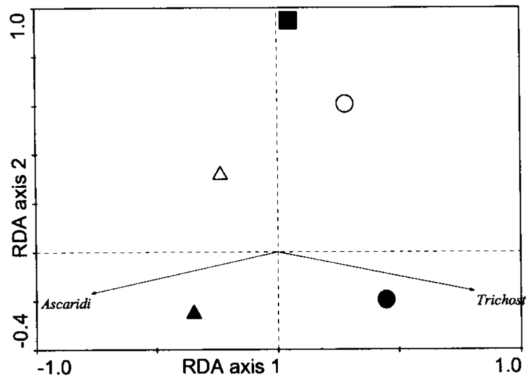

Fig. 1. A RDA ordination diagram (correlation biplot) summarising the variation in *A. compar* (denoted *Ascaridi* in diagram) and *T. tenuis* (denoted *Trichost* in diagram) infections in *L. lagopus* and *L. mutus* along a coast–inland gradient in northern Norway. Model: Y = Host * Area. Axes 1 (geographic area) and 2 (host species) account for 62.6% and 2.7% of the total variance in the parasite data, respectively. The arrows and centroids visualise the geographical differences in parasite composition in the two host species. ▲ = *L. lagopus* inland, △ = *L. mutus inland*, ■ = *L. lagopus* fjord, ● = *L. lagopus* coast, ○ = *L. mutus* coast. Note that neither *A. compar* nor *T. tenuis* were found in *L. mutus* in any of the fjord sites.

and Area 2: $\chi^2 = 15.32$, $P = 0.0001$) and intensities (Mann Whitney "U" test; Area 1: Zadj = 2.35, P = 0.02, and Area 2: Zadj = 2.25, P = 0.03) of *A. compar* were significantly higher in Willow Ptarmigan than in Rock Ptarmigan in both inland areas. In Area 7, Willow Ptarmigan had significantly higher prevalence ($\chi^2 = 13.0$, $P = 0.0003$) and intensities (Mann Whitney "U" test; Zadj = 2.49, P = 0.013) of *T. tenuis* than Rock Ptarmigan. Prevalence and intensities of *T. tenuis* were not tested between host species in Area 8 due to the low number of parasite records in Rock Ptarmigan.

During our eleven years of sampling in Area 7 *T. tenuis* showed a marked temporal variability in Willow Ptarmigan (Table 1a and 2), where prevalences varied from a minimum of 25.0 in 1998 up to a maximum of 75.4 in September 2001. Temporal variability of *A. compar* was also recorded in eight samples of Willow Ptarmigan collected in Area 1 in 1992, 1995 and 1998–2003, where prevalence varied from a minimum of 52.2 in 1998 up to a maximum of 83.3 in September 2003 (Table 3). We also resampled two of the areas used in 1992 for *A. compar* and *T. tenuis* to ensure that the parasites were still present before collecting the 2000 and 2001 winter samples. Samples of ten Willow Ptarmigan were collected in September 1999 and 2000 from a coastal island (Area 8), and in both samples *A. compar* was absent while the prevalence of *T. tenuis* was 100% in both years (as in 1992), but mean intensities (MI) (1999: MI = 118, 2000: MI = 136) exceeded the levels recorded in Area 7 (see Table 2). Willow Ptarmigan from the inland locality Area 2 were resampled in September 1999 and 2000 (n = 15 and n = 11, respectively), and the prevalence of *A. compar* was 86.7% in 1999 and 81.8% in 2000 (MI = 21.2 and MI = 13.9, respectively), but no infections of *T. tenuis* were recorded.

We did not find any *A. compar* in Willow Ptarmigan at coastal islands during winter, nor were any *T. tenuis* found in Willow Ptarmigan collected in the inland (Table 4), suggesting that no exchange of Willow Ptarmigan took place between inland and coast during the winters of 2000 and 2001. None of the Rock Ptarmigan from coastal islands were infected with *A. compar* during winter. However, we found *T. tenuis* in Rock Ptarmigan collected in the inland areas during winter (Table 4); one adult hen was infected, two juvenile birds with unknown sex had *T. tenuis*, one infection was recorded in a juvenile cock and eight infections

Table 2. Prevalence (Pr), mean intensity (MI) and range (R) of *A. compar* and *T. tenuis* in Willow Ptarmigan collected from a coastal locality, Area 7, in September 1993–2002.

		1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
	n	25	61	48	51	52	60	84	61	61	72
A. compar	Pr	0	0	0	0	0	0	0	0	0	0
T. tenuis	Pr	28.0	44.3	27.1	35.3	25.0	25.4	57.8	73.8	75.4	66.7
	MI	45.9	4.9	5.5	5.5	5.4	14.2	12.0	17.3	15.0	38.7
	R	1–186	1–24	1–18	1–32	1–21	1–132	1–138	1–306	1–126	1–494

Table 3. Prevalence (Pr), mean intensity (MI) and range (R) of *A. compar* and *T. tenuis* in Willow Ptarmigan collected from an inland locality, Area 1, in September 1995 and 1998–2003.

		1995	1998	1999	2000	2001	2002	2003
	n	32	23	17	25	38	25	30
A. compar	Pr	78.1	52.2	64.7	72.0	57.9	68.0	83.3
	MI	10.9	4.3	6.7	17.5	12.5	19.1	31.3
	R	1–48	1–16	1–23	1–53	1–58	1–73	1–117
T. tenuis	Pr	0	0	0	0	0	0	0

Table 4. Prevalences and mean intensities (given in brackets) of the parasites *A. compar* and *T. tenuis* in samples of Willow Ptarmigan (WP) and Rock Ptarmigan (RP) from inland and coast areas, collected in February/March 2000 and 2001.

	Inland 2000		Inland 2001		Coast 2000		Coast 2001	
	WP	RP	WP	RP	WP	RP	WP	RP
n	45	95	34	111	96	52	64	83
A. compar	48.9	31.6	58.8	42.3	0	0	0	0
	(4.0)	(2.1)	(4.9)	(3.5)	(–)	(–)	(–)	(–)
T. tenuis	0	4.2	0	7.2	43.8	25.0	75.0	37.3
	(–)	(2.0)	(–)	(2.4)	(9.7)	(3.2)	(10.8)	(3.5)

were found in juvenile hens. These observations suggest that no Rock Ptarmigan had dispersed from inland areas to spend winter at coastal islands, but some coastal Rock Ptarmigan, primarily juvenile hens, had dispersed to the inland during the winters of 2000 and 2001.

4. Discussion

The nematodes *T. tenuis* and *A. compar* showed a marked difference in geographical distribution between subpopulations of both Willow and Rock Ptarmigan. Geographical subdivisions like coast, fjords and inland explained more of the variability in parasite abundance than individual sampling sites within regions or host species did. The geographical distribution patterns of *A. compar* and *T. tenuis* were similar among the sympatric ptarmigan species, where *A. compar* was common in the inland, but not at the coast, while *T. tenuis* was found exclusively on coastal islands. This consistent difference in distribution patterns meets the first of five criteria suggested by MacKenzie and Abaunza (1998). The effects of host age and sex on parasite abundance were not significant in either of the two host species. Thus, distributions of the proposed tag species among hosts were not biased by host age or sex, presenting us with a model host-parasite system where the use of biological tags could be applied in a terrestrial environment.

If parasites are to be used as biological tags, candidate species have to infect a large proportion of the host population and maintain a relatively constant level of infection from year to year in order to function as a reliable tag (MacKenzie & Abaunza 1998). The coastal tag, *T. tenuis*, reached 100% prevalence in all three samples of Willow Ptarmigan collected from Area 8. However, in the coastal subpopulation sampled during the period 1992–2002, Area 7, there was a considerable variability in prevalence of *T. tenuis* ranging between 25.0%–75.4% (mean = 46.7%). *A. compar* showed slightly less temporal variability in the inland subpopulation of Willow Ptarmigan sampled for seven years following the initial survey in 1992, with prevalence ranging between 52.2%–83.3% (mean = 68.9%). In the case of Rock Ptarmigan, recorded prevalence and intensities of *A. compar* and *T. tenuis* were lower than in Willow

Ptarmigan in 1992, which is in accordance with other studies where Rock Ptarmigan typically had a lower abundance of *T. tenuis* than Willow Ptarmigan or Red Grouse (Sonin & Barus 1981, Watson & Shaw 1991). These results show that infection levels were quite variable over time, and the results of any survey attempting to use these nematodes as tags could be affected by year. In addition, prevalence was too low to estimate dispersal quantitatively, because the actual proportion of dispersing individuals will be underestimated when tag prevalence falls below 100% in the source populations. Our parasite tags would still serve as a qualitative tool capable of revealing the mere presence of dispersal along the coast–inland gradient in winter. The difficulties in making reliable quantitative predictions have been acknowledged in many studies where various proportions of hosts were uninfected by tag species, but in spite of this, few studies have aimed at evaluating the long-term variability of the parasite species (MacKenzie 1987, 2002). However, in a review of four case histories involving parasites used as tags in Pacific salmonid stock identification, Margolis (1998) recognized that parasite prevalence were too unstable to function as other than qualitative tags and stressed the need for annual re-establishment of baseline data.

In the present study, practical use of the proposed parasite tags revealed no winter dispersal of Willow Ptarmigan along a coast–inland gradient. This is in accordance with other studies on Willow Ptarmigan in Fennoscandia, where mainly short-range movements were recorded (Myrberget 1976, Pedersen *et al.* 1983, Smith 1997). In Rock Ptarmigan shot at coastal islands during the winters of 2000 and 2001, there were no findings of *A. compar*. Among Rock Ptarmigan shot at inland localities, we found some hosts infected with *T. tenuis* in the winter samples both in 2000 and 2001, suggesting that these hosts must have originated from a coastal area. With one exception, all hosts found positive for *T. tenuis* at inland areas were juvenile birds, and the majority of these were juvenile hens. This may indicate that juvenile Rock Ptarmigan hens were the most likely to disperse along the coast–inland gradient investigated in this study. In an earlier, limited study where Rock Ptarmigan chicks from a coastal island were wing tagged in Troms County, N. Norway, four recoveries were made, among these was a juvenile hen shot in one of our inland study localities (Myrberget & Bugge 1974). In Iceland, differential migration produced a difference in the proportion of sexes encountered at different places in winter, where more females than males left their breeding grounds moving south- or eastwards during late autumn or early winter (Gardarsson 1988). Cocks were more reluctant to leave breeding grounds in Iceland, which may be the case in Norway too, because none of the adult inland Rock Ptarmigan cocks had infections of *T. tenuis* in winter. Thus, use of parasite tags indicated the presence of a coast to inland dispersal of Rock Ptarmigan during winter.

One of the prerequisites listed by MacKenzie and Abaunza (1998) was that the parasite species used as tags should not induce host mortality or changes in host behavior. There is evidence that *T. tenuis* may increase mortality in Red Grouse and influence host behavior (Hudson 1992, Hudson *et al.* 1998), but the intensities encountered in our ptarmigan study populations were much lower than levels expected to induce mortality in Red Grouse (Hudson 1992). In the case of *A. compar*, little is known about pathogenic effects in ptarmigan, but there are some evidence indicating that *A. compar* may be connected to cyclic population fluctuations by reducing breeding production in Rock Partridges (Rizzoli *et al.* 1999, Tompkins *et al.* 2002).

We used the mature stages of two endoparasite species as tags and their detection required that hosts were dissected to obtain information on infection status. However, this study represents an integral part of a larger study focussing on the temporal variability of taxonomically very different ptarmigan endoparasite species (see Holmstad & Skorping 1998, Holmstad *et al.* 2003). As a consequence, we had to collect subsamples of different host populations in order to obtain reliable, quantitative data on individual hosts and their parasite infections. This does not imply that the use of parasite tags are restricted to game species or birds that died of natural causes. A non-invasive approach would indeed be possible by collecting faecal samples from hosts, which could be examined for eggs or larvae belonging to distinguishable parasite species with known geographical distributions. Such an approach would have been readily applicable in our study, if the sole purpose of sampling was to reveal ptarmigan dispersal, because there were only one species of each proposed tag belonging to very different nematode families with characteristic transmission stages. Thus, the potential use of parasite tags should be applicable in studies on a range of other birds that are not subject to hunting.

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Loisten esiintymisen käyttö lintujen levittäytymisen tutkimuksessa: kiirunoiden ja riekkojen talviaikainen dispersaali Pohjois-Norjassa

Loisten esiintyminen voi antaa arvokasta tietoa isäntälajin ekologista. Kirjoittajat tutkivat Pohjois-Norjassa kahden sukkulamadon, *Ascaridia compar* ja *Trichostrongylus tenuis* alueellista ja ajallista esiintymisen vaihtelua riekon ja kiirunan mahassa sekä suolistossa. Aineisto koostui 151 riekkonäytteestä ja 199 kiirunanäytteestä, jotka oli kerätty kuudelta eri maantieteelliseltä osa-alueelta. Isäntälajin iällä tai sukupuolella oli vain vähän vaikutusta infektion esiintymiseen.

A. comparin esiintyminen vaihteli sisämaassa 52,2–78,1 % kuuden tutkimusvuoden aikana syyskuussa kerätyissä näytteissä. *T. tenuisin* esiintyminen vaihteli rannikkoalueella 25,0–75,4 % kymmenen tutkimusvuoden aikana kerätyssä aineistossa. Molempia loislajeja tavattiin useammin riekoissa kuin kiirunoissa. Loislajien syyskuinen esiintyminen erosi maantieteellisesti merkittävästi toisistaan, *A. compar* oli yleinen sisämaassa, kun taas *T. tenuista* tavattiin vain rannikkoalueella.

Loisten esiintymiskuva viittaa siihen, että kiirunat, erityisesti nuoret naaraat, levittäytyvät talvella rannikolta sisämaahan. Vastaavaa ei havaittu tapahtuvan riekoilla. Artikkelin lopussa kirjoittajat pohtivat loisten käyttömahdollisuuksia biomarkkereina ja sukkulamatojen käyttöä kiirunoiden sekä riekkojen levittäytymisen tutkimuksessa.

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