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Linked seasonality between a phoretic mite and its moth fly host (Parasitiformes: Mesostigmata and Diptera: Psychodidae)

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Original research

ABSTRACT

Phoresy is a widespread phenomenon in mites. It allows mesostigmatid mites that are associated with ephemeral habitats such as mammal dung to travel fast on larger animals that can detect a proper habitat from a greater distance. To address the gap in knowledge on phoresy in these mites, we examined host specificity in phoretic Mesostigmata associated with psychodid species and studied temporal dynamics to see if phoretic life cycles are synchronized with the host life cycle. Using a field collection of more than 2500 moth flies (Psychodidae) from eight localities in Norway, we found three out of 29 species carrying phoretic mites of two species: deutonymphs of *Trachygamasus ambulacralis* were phoretic on female *Psychoda phalaenoides* and both sexes of *Psychoda grisescens*, and adults of *Iphidozercon gibbus* were phoretic on females of *Psychoda satchelli*. All flies were species with larval development in vertebrate dung. Abundances of *P. phalaenoides* and *T. ambulacralis* were highly correlated, probably due to the two species exhibiting similar seasonal variations in abundance; both were significantly seasonal with a peak in August and September. Thus, *T. ambulacralis* infestation levels on *P. phalaenoides* appeared similar throughout the season. We discuss the implications for the life histories of the mites in question. *Trachygamasus ambulacralis* is first time recorded from Norway.

Keywords symbiosis; commensalism; phenology; coprophagy; phoresy; biological interactions

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Introduction

The term "phoresy" was introduced by the French entomologist Pierre Lesne in 1896, referring to phenomena when a smaller animal (the phoretic) is transported by a larger one (the host or carrier) (Walter and Proctor, 2013). Many other definitions have been proposed since then, but none of them has yet been commonly accepted (Walter and Proctor, 2013). For example, Farish and Axtell (1971) restricted phoresy to the situations when the phoretic actively seeks the host, attaches to its outer surface for a limited period of time, and ceases feeding and ontogenesis during the attachment. Athias-Binche (1991) added to this definition that the phoretic must be quiescent when on the host. Houck and O'Connor (1991) disagreed with the opinion that the phoretic must be active when searching for the host, as some mites are not, and stated that phoresy takes place when the phoretic receives an ecological and evolutionary advantage when migrating to a new habitat, but cannot feed or develop when on the host. In turn, Walter and

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Proctor (2013) came back to a broader meaning of phoresy, defining it as a type of temporary symbiosis that allows a smaller individual to travel on a larger individual. In such understanding the phoretic can also feed or develop during the transportation. Phoresy might be facultative, depending on the population density or environmental perturbations, or obligatory, when it takes place in a relatively stable habitat, and the mites follow a seasonal migration cycle using traditional carriers (Krantz, 2009).

Phoresy can be found in all groups of Acariformes mites, but among Parasitiformes it is known only in Mesostigmata. Here, it is a widespread phenomenon, with over 1700 species associated with arthropods, mainly (95%) with insects (Hunter and Rosario, 1988). As a rule, mesostigmatid mites are associated with insects that live in nutritionally rich but ephemeral habitats, like mammal dung, decaying vegetation, carrion, or temporary ponds (Hunter and Rosario, 1988). The benefit of this relationship to the mites is obvious; they are small, wingless, and with sensory organs of a limited range, so they take advantage of travelling fast on larger animals that can detect a proper habitat from a greater distance (Walter and Proctor, 2013). For example, moth flies (Psychodidae) can easily detect fresh dung on which their larvae feed, and mesostigmatid mites travelling with them will achieve the same goal, finding there rich food sources: immature stages of insects or other mites and nematodes (Floate, 2011). For insects the presence of phoretic mites is usually neutral, but in few cases a mutualistic interaction between Mesostigmata and insects has been proved; the phoretic had a positive effect on host fitness by reducing the level of parasites (Walter and Proctor, 2013).

The relations between the mites and the insects are fascinating for many reasons, and draw attention of quite many acarologists, in particular to answer evolutionary and ecological questions (Walter and Proctor, 2013). Mites are considered one of the best, if not the best, group to study phoretic species associations (Klompen, 2009). Sometimes several different species (even 12) can be found on one insect (McGarry and Baker, 1997), but some mite species have a close association with a single host. In that case the phoretic has a life cycle synchronized with the life cycle of the host (Hunter and Rosario, 1988). Particularly in temporary habitats such as dungpats and carrion this is an advantage, because the mites dependent on such habitat must be moved from one place to another regularly and predictably in their life cycle. Usually, only one life-history stage is phoretic in a given species (Walter and Proctor, 2013), and in most cases phoresy is restricted to the deutonymphs or adult females (Krantz, 2009).

Among the Diptera, 19 families have been found to transport mites, and the most common is the Muscidae, followed by Sphaeroceridae and Psychodidae (Hunter and Rosario, 1988). Regarding the latest family, there is still a lack of information about the phoretic interactions with mites on the species level, so our aim was to fill this gap. We here present the first population-level data on Psychodidae and Mesostigmata interactions based on standardised collection throughout the field season, and use them to test the hypotheses that 1) interactions between Mesostigmata and Psychodidae are host specific, in which particular phoretic species are confined to particular hosts, and 2) the life cycles of the phoretics are synchronized with the life cycle of the host.

Material and methods

Study area

All material examined in this study was collected using Malaise traps on eight minerotrophic rich fens in Hedmark county, east Norway (Figure 1, Table 1). The study aimed at inventorying aquatic and semiaquatic insects of many different groups (analogous to Ekrem *et al.*, 2012), but non-aquatic representatives of the families in question were also collected. Detailed descriptions of localities (in Norwegian) can be read at www.naturbase.no, see Table 1 for links.

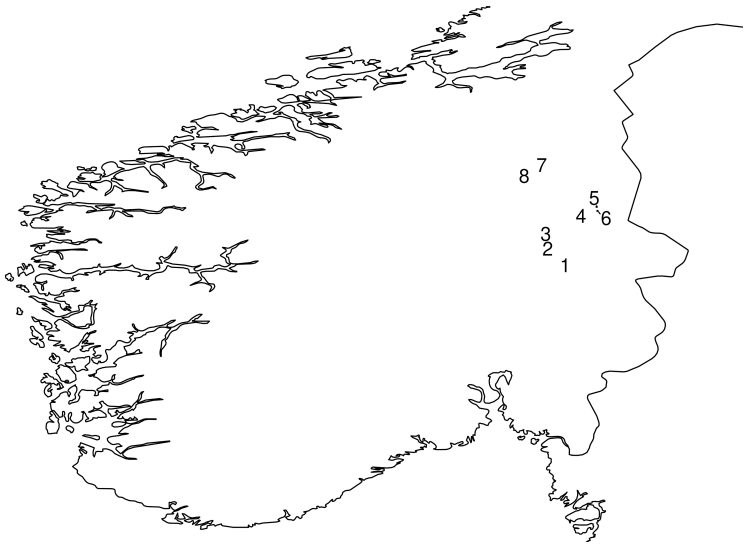


Figure 1 Map of localities sampled during the rich fen project.

Sampling and identification

Moth flies were identified using the reference collection in the University Museum of Bergen (most specimens are listed in Andersen and Håland, 1995, Kvifte *et al.*, 2011, Kvifte and Andersen, 2012, Kvifte and Boumans, 2014 and Kvifte, 2019), as well as illustrations and descriptions in Withers (1989), Tonnoir (1922, 1940) and Ježek (1983, 1990). Some females were identified by associations with males and/or DNA barcoding following methods described in Ekrem *et al.* (2012). In the present paper we only present results from the species found to carry phoretic mites.

Mesostigmata mites were preserved in 70% ethyl alcohol, and mounted on permanent slides in Hoyer's medium. They were identified to species level, using universally applied keys (Ghilyarov and Bregetova, 1977; Hyatt, 1980; Karg, 1993; Kalúz and Fenda, 2005; Gwiazdowicz, 2007). The information on the Mesostigmata of Norway is based on the checklist (Gwiazdowicz and Gulvik, 2005a) and later references (Gwiazdowicz and Gulvik, 2007; Gwiazdowicz *et al.*, 2013; Bolger *et al.*, 2018; Seniczak *et al.*, 2019, 2020, 2021a,b).

Table 1 Localities sampled during the rich fen project

Locality number	County	Municipality	Locality name	North	East	Area of fen (daa)	Elevation	Habitat type	Naturbase link	First trap deployment	Final trap collection	Number of collection
1	Innlandet	Åmot	Kildesaga	61.178778	11.402167	6.8	270	Forested rich fen	https://faktaark.naturbase.no/?id=BN00075142	28.Apr.2016	27.Oct.2016	14
2	Innlandet	Stor-Elvdal	Nabbtjern	61.378417	11.191750	116.7	260	Open loose bottom fen surrounding lake	https://faktaark.naturbase.no/?id=BN00026540	29.Apr.2016	27.Oct.2016	13
3	Innlandet	Rendalen	Sekserbua NØ	61.556056	11.168556	61.3	522	Open firm bottom fen	https://faktaark.naturbase.no/?id=BN00026412	27.Apr.2016	27.Oct.2016	13
4	Innlandet	Rendalen	Jøgåsmyra	61.774556	11.593472	694.4	640	Open calcium carbonate fen	https://faktaark.naturbase.no/?id=BN00026324	13.May.2016	27.Oct.2016	12
5	Innlandet	Engerdal	Ulvåkjølen-Sundsetra	61.836556	11.791250	2,402.7	662	Open rich fen	https://faktaark.naturbase.no/?id=BN00026842	28.Apr.2016	27.Oct.2016	13
6	Innlandet	Engerdal	Åsen	61.885861	11.782833	18	691	Spring fen	https://faktaark.naturbase.no/?id=BN00026819	13.May.2016	27.Oct.2016	12
7	Innlandet	Tolga	Bjørvollen N	62.387028	11.118861	335.2	774	Alpine mosaic rich fen	https://faktaark.naturbase.no/?id=BN00099251	13.May.2016	27.Oct.2016	12
8	Innlandet	Tynset	Brydalskjøle n	62.255444	10.907250	990.4	781	Alpine mosaic rich fen	https://faktaark.naturbase.no/?id=BN00100041	13.May.2016	27.Oct.2016	12

Specimens in ethanol and on microscope slides are deposited in the entomological collections, University Museum of Bergen (ZMUB).

Statistical analysis

Statistical analyses were conducted in R version 3.4.3 (R Core Team, 2017). We used the base R functions *cor.test* to test for correlations in associations between flies and mites and *glm* to test for statistical significance of explanatory variables. All analyses were done individually for each locality and for all localities pooled together. For testing seasonality of associations, we treated fly and mite specimen counts as the poisson distributed response variable with site ID and the polynomial of sampling event number (collection event 1, collection event 2, etc.) as explanatory variable in a generalised linear model. All models were found to be overdispersed and we therefore assessed significance using an F-test in a quasi-poisson approach. To test seasonality of the association between mites and flies we treated a table of infested *vs* uninfested flies as a binomially distributed response variable with time and site ID as predictors.

Results

A total of 2593 specimens of Psychodidae belonging to an estimated 29 species were identified, of which 1198 belonged to the genus *Psychoda*; three species in this genus were found to carry mites, namely *Psychoda phalaenoides* (L., 1758), *Psychoda grisescens* Tonnoir, 1922 and *Psychoda satchelli* Quate, 1955. Together, these species made up over 50% of all *Psychoda* individuals collected in the samples, with counts of 354, 37 and 227 identified specimens, respectively. These species are all widespread and common in the Norwegian Psychodidae fauna (Kvifte *et al.*, 2011).

Two species of mites were identified: deutonymphs of *Trachygamasus ambulacralis* (Willmann, 1949) that made up over 90% of mites found in this study, and females of *Iphidozercon gibbus* (Berlese, 1903). *Trachygamasus ambulacralis* has not previously been recorded from Norway; *I. gibbus* was recorded by Gwiazdowicz and Gulvik (2005b) based on a male and three females from Sogn og Fjordane county. All identified mites were found to be phoretic, and those that were still hanging on to their hosts were attached by means of the chelicerae to the first three abdominal segments of the fly. For numbers of infested and uninfested flies throughout the seasons per locality, see Table 2.

Table 2 Abundance of coprophagous Psychodidae and phoretic Mesostigmata on each of the eight sampled localities

	Locality 1	Locality 2	Locality 3	Locality 4	Locality 5	Locality 6	Locality 7	Locality 8
Diptera								
Psychoda phalaenoides								
Total number of specimens	56	24	42	4	97	107	16	8
Specimens with observed phoretic mites	2	6	4	0	7	6	3	3
Psychoda grisescens								
Total number of specimens (males only)	4	2	2	0	6	7	11	5
Specimens with observed phoretic mites	0	0	0	0	0	3	2	0
Psychoda satchelli								
Total number of specimens	17	13	21	4	86	83	1	2
Specimens with observed phoretic mites	0	0	1	0	3	0	0	0
Other *Psychoda*	116	48	134	0	68	146	5	26
Mesostigmata								
Trachygamasus ambulacralis	5	8	8	0	10	15	7	6
Iphidozercon gibbus	0	0	1	0	4	0	0	0

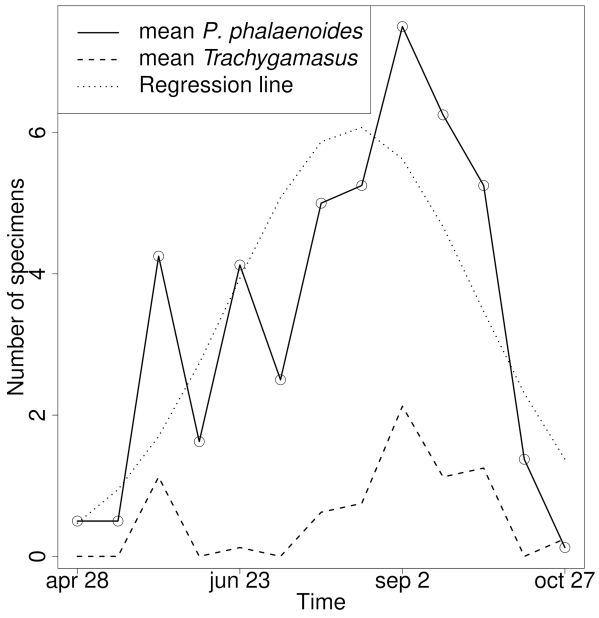


Figure 2 Mean abundance of *Psychoda phalaenoides* and *Trachygamasus ambulacralis* through the 2015 season. The regression line shows predicted abundance of *P. phalaenoides* as a function of time, according to the *glm* described in the text.

The most frequent host of phoretic deutonymphs of *Trachygamasus ambulacralis* were *Psychoda phalaenoides* females (n=29). This mite species was also occasionally found on males of *P. phalaenoides* (n=2) and both sexes of *P. grisescens* (total number unknown due to ambiguous identifications of females). Females of *Iphidozercon gibbus* were phoretic on male *P. satchelli* (n=4) and female *P. phalaenoides* (n=1).

Due to low specimen numbers, *I. gibbus*, *P. grisescens* and *P. satchelli* could not be analysed quantitatively. Peaks of abundance in *T. ambulacralis* generally coincided with those of *P. phalaenoides*, although *P. phalaenoides* also displayed some peaks unassociated with *T. ambulacralis* (Figures 2, 3). The two abundances were strongly correlated when all sites and sampling intervals were pooled together ($r^2 = 0.445$, $P < 0.00001$, Figure 2); significant correlations were also found on fens Bjørvollen ($r^2 = 0.706$, $P = 0.007$), Brydalskjølen ($r^2 =$

Table 3 Summary statistics for statistical models used in the analysis

	Degrees of freedom	Deviance	Residual degrees of freedom	Residual deviance	P-value	Modeled distribution
GLM 1: Abundance of Psychoda phalaenoides *by site and sampling event*						quasipoisson
Locality	7	254.7	96	372.29	2.451e-12	
Time (polynomial)	2	121.8	94	250.49	5.305e-09	
GLM 2: Abundance of Trachygamasus gracilis *by site and sampling event*						quasipoisson
Locality	7	22.89	96	168.41	N.S.	
Time (polynomial)	2	23.76	94	144.64	0.01	
GLM 3: Proportion of Psychoda phalaenoides *carrying phoretic* Trachygamasus gracilis *by site and sampling event*						binomial
Locality	7	16.98	54	58.86	0.01	
Time (polynomial)	2	1.51	52	57.36	N.S.	

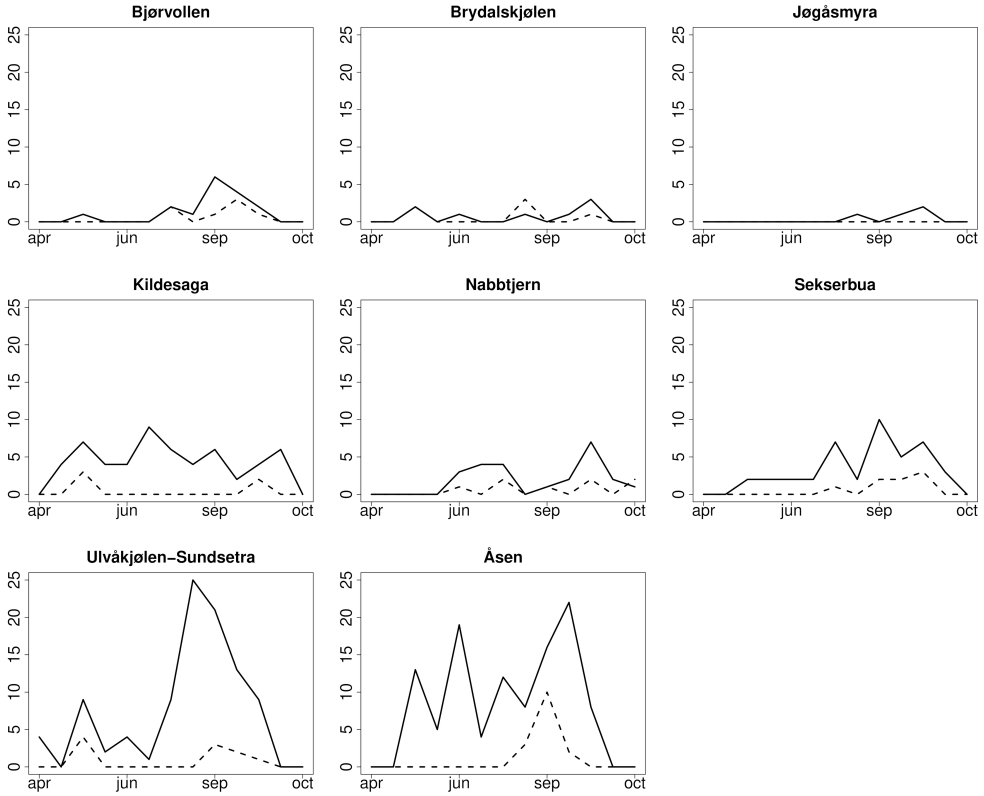


Figure 3 Abundance of *Psychoda phalaenoides* (solid line) and *Trachygamasus ambulacralis* (dotted line) for each of the eight rich fens.

0.566, P = 0.043), Nabbtjern (r^2=0.588, P = 0.034) and Sekserbua (r^2 = 0.824, P < 0.001).

Seasonal variance in abundance was found to be significant for both *P. phalaenoides* (F-test of quasi-poisson model with site ID and 2-polynomial time since start of sampling, P = 5.30 x 10^{-9}) and *T. ambulacralis* (Chi-test of poisson model with 2-polynomial time since start of sampling, P = 6.90 x 10^{-6}). There were also significant differences between sites both for abundance of *P. phalaenoides* (P = 2.45 x 10^{-12}) and *T. ambulacralis* (P = 0.0017). No evidence was found for the association between the two species varying throughout the season, but there were significant differences in infestation rates between sites (p=0.017). Also, no significant relationships were found between latitude and abundance for any of the species. For further details of the GLMs, see Table 3.

Discussion

These are to our knowledge the first phoretic associations of identified Psychodidae with identified Mesostigmata from Europe, however, several previous associations have been documented from other regions or with lower taxonomic resolution.

Whitsel and Schoeppner (1973) identified two species of *Iphidozercon* (*I. californicus* Chan, 1963 and *Iphidozercon* sp.) as phoretic on *Psychoda satchelli* in California; in our study we identified *I. gibbus* from the same nominal species. Withers (1988, 1989) considered *P. satchelli* as a synonym of *P. albipennis* Zetterstedt, 1850 and listed sewage beds, rotten vegetation, bird and bat guano, carnivore and ruminant dung and polyporous fungi as recorded breeding habitats for their saprophagous larvae. *Iphidozercon gibbus* also occurs in many different decaying habitats including bird and rodent nests (Kalúz and Fenda, 2005; Gwiazdowicz, 2007) from or

to which it probably migrates, at least with *P. satchelli*.

Lundqvist (1998) identified deutonymphs of *Trachygamasus gracilis* Karg, 1965 as phoretic on unidentified *Psychoda* sp. in Southern Sweden, and further identified *T. ambulacralis* deutonymphs from fly trap residues. We deem it likely that his *Trachygamasus* records predominantly are from *P. phalaenoides* and other dung-breeding psychodids, as these are very common in Southern Sweden (Svensson, 2009) and furthermore overlap with *Trachygamasus* in habitat.

Interestingly, the psychodid species that *T. ambulacralis* attach to are also the ones most commonly found within inflorescences of the plant *Arum maculatum* L., 1753 (Espíndola *et al*., 2011). This plant attracts *P. phalaenoides* females and *P. grisescens* of both sexes using chemical mimicry of these insects' larval habitats, and relies on these flies for pollination. The sex ratios of these pollinators seem to follow the same pattern as the hosts of *T. ambulacralis*– predominantly *P. phalaenoides* females and *P. grisescens* of both sexes. The difference in sex ratios between these two species could possibly reflect different mating systems in the two species: *P. phalaenoides* males have been inferred to locate females with species-specific pheromones (Yeargan and Quate, 1996), meaning mating can take place anywhere and the only individuals who will actively seek out larval development substrates will be females. No behavioral data is available for *P. grisescens*, but their males may well locate females directly on the larval habitats.

In Mesostigmata some of species use the deutonymphs (e.g. in Sejida, Uropodina and Parasitiae) for the phoretic dispersal while in others (Trigynaspida and derived Dermanyssiae) females are typical phoretics (Walter and Proctor, 2013). The use of the last nymphs could be explained with their greater resistance to harsh environmental circumstances and ability to delay the last moult until appropriate conditions are available (Rapp, 1959; Walter and Proctor, 2013). It is likely that it also prevents inbreeding during transport which would be possible with both males and females present on the same host individual. That could be true for *T. ambulacralis.* In case of *I. gibbus*, in which males are very rare when compared to females (e.g. Gwiazdowicz, 2005, 2007), phoresy of females could be more effective in terms of reproduction when transported to the new habitat, however, biology of both mite species mentioned in this work is virtually unknown.

The phoretic associations between Mesostigmata and Psychodidae are in our opinion likely to be phylogenetically recent ecological associations rather than co-cladogenetic macroevolutionary relationships. The *Psychoda* species encountered as phoretic hosts in this study are phylogenetically distant from each other (Cordeiro, 2013; Kvifte, unpubl. data; see also genetic distances in Kvifte and Andersen, 2012) and both *T. ambulacralis* and *I. gibbus* have been previously found in phoretic association with other coprophagous Diptera such as the ceratopogonid *Culicoides obsoletus* (Meigen, 1818) (Mašán and Országh, 1994). Interestingly many dung-associated *Psychoda* have not been observed with mites; and psychodids breeding in other habitats than dung have not to our knowledge been associated with Mesostigmata. Nevertheless, the *T. ambulacralis / P. phalaenoides* relationship shown herein may be indicative of the latter species being the "primary" phoresy host of *T. ambulacralis,* and it is worthy to emphasize that *I. gibbus* females mainly infested other hosts (*P. satchelli*) than those used by *T. ambulacralis*.

For both mite species found associated with Psychodidae in this study, the association is likely motivated by their need to colonise the patchy and ephemeral habitats that the host fly actively seeks out. Association studies such as the present one are, however, only the first step in understanding the fascinating evolutionary phenomenon of phoresy, and future studies should address the short and long term benefits and disadvantages for both parts of the association, its dynamics and the behavioral triggers for mounting and dismounting.

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Author contributions

GMK planned fieldwork with colleagues at the University Museum of Bergen. GMK conceived of the study, identified psychodids, performed statistical analyses and prepared figures. AS coordinated identification of mites and conducted background research in phoresy. SK and TM identified mites and performed observations on their phoretic modes. GMK and AS wrote the paper, all authors approved the final version.

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