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Tychus normandi Jeanell, 1950 and *Tychus monilicornis* Reitter, 1880 (Staphylinidae: Pselaphinae) in a coastal fen in Mecklenburg-Western Pomerania, Germany – distribution, habitat preference, and phenology of two extremely rare species

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The minerotrophic coastal paludification fen in the 'Heiligensee and Hütelmoor' nature reserve northeast of Rostock, which is aperiodically influenced by brackish water from the Baltic Sea during storm surges, was investigated for two years using pitfall trap series (PTS). Six to eight pitfall traps per PTS were operated from May to October at six sites 2020 and eight sites 2021 with fortnightly emptying. Remarkably, the extremely rare species threatened by extinction *Tychus normandi* Jeanell, 1950 and *T. monilicornis* Reitter, 1880 were regularly caught in almost all the sites surveyed. In 2020, 4405 individuals (ind.) of rove beetles were captured in 171 species, including *T. normandi* in 131 ind. and *T. monilicornis* in 15 ind. In 2021, 4842 ind. were captured in 143 species, of which *T. normandi* in 195 ind. and *T. monilicornis* in 23 ind. Their activity peaked from late May to late June. In 2021, the proportion of ♂ of *T. normandi* was 83.6 %, that of *T. monilicornis* 73.9 %. For clarification whether the *Tychus* species exhibit a salt preference, three soil cores each were analyzed for salinity on each of the eight sites surveyed in 2021 and one reference site in June 2022. The sites investigated had a salt content of 75-867 mg/100 g soil. There was no evidence of a salt preference for either *Tychus* species; thus, they are apparently halotolerant. The dynamic and constant water supply of intact *Phragmites* reedbeds in the nature reserve as well as mesoclimatic effects may be crucial for the occurrence of both hygrophilous species. Salt grassland management, here late summer mowing, reduces the habitat suitablility for both species.

Keywords: fen, rove beetles, habitat requirements, *Phragmites*, salt tolerance, phenology

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INTRODUCTION

The small (1.5-1.7 mm) pselaphine beetles *Tychus normandi* Jeanell, 1950 and *T. monilicornis* Reitter, 1880 are widespread in Europe (Schülke & Smetana 2015). In northern Germany, they are among the faunistic peculiarities (see http://www.colkat.de for an updated distribution map). There is no record of *T. normandi* in Schleswig-Holstein, and *T. monilicornis* is very rare (Gürlich et al. 2017). In the Lower Elbe region, *T. normandi* is extremely rare, and *T. monilicornis* has not been recorded (Gürlich et al. 2017). For Mecklenburg-Western Pomerania (M-V), *T. normandi* was recently reported for the first time, and *T. monilicornis* for the second time (Kleeberg 2023). In contrast, *T. niger* (Paykull, 1800) is one of the more common and widespread species in M-V (Kleeberg 2023). In the Heiligensee and Hütelmoor nature reserve, herafter called NHH, they were recorded in large numbers and repeatedly (Lindner et al. 2025). This provides an opportunity to focus on the occurrence, habitat preference and phenology of both rare species in a coastal fen, that has been intensively studied in terms of its development and characteristics.

The post-glacial land subsidence and the eustatic sea-level rise, both in conjunction with coastal equalization processes, led to the formation of fens in the southern Baltic Sea region, which were aperiodically flooded by the Baltic Sea. Today recognized as an independent fen type 'coastal fen' (Jeschke 1983). Due to the influence of brackish water, the potential natural climax vegetation is the *Phragmites* reed (Kopp et al. 2005), not forest. Extensive grazing led to the development of large areas of salt grassland from the 13th century onwards. The coastal saltmarshes and grasslands originally covered approx. 21,000 ha in M-V. Extensive, largescaled melioration (Kirchner 1971) and embankments as well as subsequent intensive cultivation (between 1960 and 1990) led to an approx. 91 % reduction of the original area (Succow & Joosten 2001).

The NHH has also been heavily affected due to the agricultural politics of the German Democratic Republic (1949-1990). Despite its special character as a coastal marsh and its legal status as National Protected Area (NPA) since 1957, it has been subject to complex melioration and intensive agricultural use (Krischer 1977, Pommeranz 1999, Stock 2005). With the efforts of the peatland protection program that began in the 1990s (e.g. Lenschow 1997, Lenschow & Thiel 2000), measures for its rewetting were also implemented in the NHH. In connection with this, the NHH was intensively studied entomologically (e.g. Schmidt 1994, Frase & Wolf 2011, Lindner et al. 2025), geologically and hydrologically (e.g. Selle et al. 2016, Miegel et al. 2016, 2017, Schreiber et al. 2021). As part of the Natura 2000 Area "Wälder und Moore der Rostocker Heide" (DE 1739 – 304) the NPA is integrated in the European protected areas network.

As the only known localities of *Tychus normandi* and *T. monilicornis* in M-V are located along the Baltic Sea coast (Kleeberg 2023), partly in oligohaline coastal wetlands, a certain salt tolerance can be expected. A possible salt affinity can be tested within the salinity gradient of the NHH. Among rove beetles, there are halobionts (obligatory bound to saline biotopes), halophiles (facultative inhabitants of saline biotopes with a pronounced affinity for salinity), haloxenes (halotolerant species without pronounced affinity for salinity) and those that occur accidentally in coastal or near-coastal areas (Majka et al. 2008, Irmler & Lipkow 2018). A stenotopic salt binding can be excluded based on the overall distribution of the species, though there must be other factors influencing the unusual regional species distribution.

The distribution pattern might be explained by the special maritime climate in the proximity of the Baltic Sea shore and microclimatic effects of the vegetation. Additionally, changing environmental conditions due to human influence, especially land use, have a strong impact on the occurrence and adaptation of invertebrates (e.g. Dittmer & Schrader 2000, Lübke-Al Hussein et al. 2008). Thus, the present study considers the land use history and area development of the NHH over the last century, characterizes the current state regarding the occurrence and habitat preference of *Tychus normandi* and *T. monilicornis*, deals with their seasonal occurrence and investigates the question of whether a salinity preference or mesoclimatic binding may exist.

MATERIAL AND METHODS

Study area

The 490-hectare Heiligensee and Hütelmoor nature reserve (NHH) is part of the lowland along the Baltic Sea coast northeast of Rostock and Markgrafenheide. The peatland originally developed as a minerotrophic paludification fen that later came under influence of the Baltic Sea in the course of the litorina transgression (Schmidt 2003, Miegel et al. 2016). Until the enforcement of the dune dyke between 1963 and 1967, Lake Heiligensee was connected to the Baltic Sea by an inlet and return channel, but under the embankment it then gradually turned to a freshwater system (Krischer 1977). Beginning in the early 1970s, intensive grassland management was practiced in the NHH and the fen was drained via a pumping station. From 1976, mainly field grass was cultivated, enhanced by ploughing up the peat, subsequent reseeding and intensive fertilization (Stock 2005, Selle et al. 2016). Through the removal of the pumping station in 1993 and the creation of a sill at the areas water outlet, the lowland was rewetted with freshwater, with a tendency towards increasing water levels since 1993 and a sharp rise in 2009 with effects on evaporation, retention and runoff (Miegel et al. 2016).

The semi-circular coastal fen (Fig. 1) is subject to an aperiodic influx of Baltic Sea's brackish water. High water levels in the Baltic Sea lead to episodic flooding of the lowland area due to backwater in the draining ditches (backwater via the Breitling) and can cause salt intrusion (Miegel et al. 2017, Schreiber et al. 2021). In addition, storm surges, some of them severe, generated by wind backwater effects led to breaches in the dune dyke and, as in 1995, to the complete flooding of the area. Documented storm surges with salt ingress were recorded in 1872, 1904, 1913, 1949, 1954, 1995 (Selle et al. 2016) and 2017 (Miegel et al. 2017). In addition, flooding from the catchment area of the watercourses is possible, whereby the lowland itself has a considerable retention effect (Miegel et al. 2016). In the long term, the natural erosion of the abandoned dune dyke in front of Lake Heiligensee (Fig. 1) will probably result in the formation of a bay (Miegel et al. 2016).
The NHH is situated in the transition zone between the maritime western and continental climate of Eastern Europe, i.e. it is influenced by both maritime (relatively balanced temperature regime) and continental factors. Compared to the inland, it has slightly lower summer and higher winter temperatures, a later onset of spring and summer, higher humidity and a greater number of stormy days. The lowland itself is locally sheltered from the wind; favored by the adjacent forest and the dune dyke towards the Baltic Sea (Miegel et al. 2016, 2017).

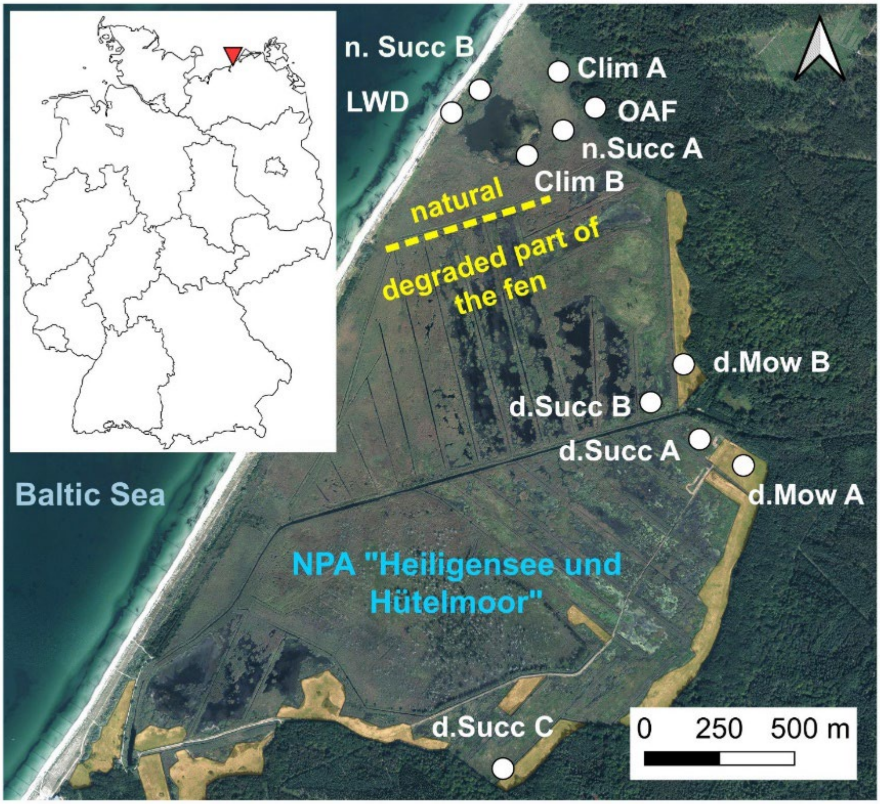

Fig. 1: Aerial view of the minerotrophic coastal paludification fen in the 'Heiligensee and Hütelmoor' nature reserve near Rostock, Mecklenburg-Western Pomerania, Germany. Pitfall trap series are marked with white dots (for site descriptions see Tab. 1) and site-codes; mown areas are highlighted in pale yellow; the dashed line marks the margin between the part of the fen that was rewetted after heavy degradation by melioration and intensive agricultural use and the unmeliorated, near natural part of the fen.

Research programme and brief characterization of the sites

From April to October (19/04/-18/10/2020 and 18/04/-17/10/2021) 6-8 pitfall traps (PT, transparent 300 ml polypropylene plastic cups, ~7 cm opening width, trapping liquid: 100 ml salt solution with detergent) per PT series (PTS, minimum distance between traps 10 m) were installed, emptied every 14 days accompanied by the replacement of the trapping liquid. The catch was preserved as a pooled sample for each sampling interval and PTS in 80 % ethanol (Lindner et al. 2025). The number of active PT collected was documented for the calculation the 14d activity density ADI_{14d} (equ. 1). Six sites were sampled in 2020, and eight in 2021 (Table 1). Three sites were sampled repeatedly as a reference over the years and land use gradient.

Tab. 1: Brief characterization of the areas surveyed in 2020 and 2021 with pitfall traps in the 'Heiligensee and Hütelmoor' nature reserve (cf. Lindner et al. 2025).

Site	Year	Brief characterization of pitfall traps sites
degraded (d) part of the fen: heavily decomposed peat due to former complex melioration and intensive agricultural use, rewetted in 1990ies, persisting drainage ditches		
Mowed meadows (mowed since 2014)		
d-Mow A	2020, 2021	Mosaic of rush, sedge and reed beds, floodplain grassland and open swales - late summer to spring short-grassed
d-Mow B	2021	
Fallow land (extensively grazed 1991-2005, abandoned since then)		
d-Succ A	2021	Mosaic of rush, sedge and reed beds, flood meadows and open swales - vegetation height 1-2 m all year round, open on disturbed areas
d-Succ B	2020, 2021	
d-Succ C	2021	Rush and sedge reedbeds, vegetation height > 1 m all year round
near-natural (n) preserved part of the bog with slightly decomposed peat soils		
Fallow land (extensively grazed 1991-2005, abandoned since then)		
n-Succ A	2021	Reed and sedge reed beds - vegetation height 1-2 m all year round, open on disturbed areas
natural succession (without use for at least 70 years)		
n-Succ B	2020	Lake Heiligensee stormsurge breakthrough site: sparse reed and rush reeds on sanded peat - vegetation height 1-2 m all year round, open on disturbed areas
Climax reed beds (not used for at least 70 years)		
Clim A	2020, 2021	wet, eutrophic *Phragmites* reedbed, reed dominance > 90 %, vegetation height 1-2 m all year round, open on disturbed areas
Clim B	2021	
Sites on the edge of the fen to complete the range of sites		
LWD	2020	Lee of the white dune (remains of the dune dyke)
OAF	2020	Oak-alder wet forest

The peat body of the NHH consists of moderately to heavily decomposed reed peat, which is predominantly between 1 m and 2 m thick and is heavily mineralized and rooted near the surface (Miegel et al. 2016). The soil type Anmoorgley predominates in the lowlands and Moorgley near the coast. The peat decomposition caused by melioration led to land subsidence of several decimeters, leaving large areas of the fen permanently flooded. The peat decomposition and land subsidence led to an alteration of the hydrological properties of the soils. In the near-natural part of the NHH, pristine, weakly degraded reed peat of up to 2.5 m thickness can still be found (Toro et al. 2022).

The wetland is dominated by stands of reed *Phragmites australis*, (Cav.) Trin. ex Steud.

alongside beach sedge *Bolboschoenus maritimus*, (L.) Palla and salt pond rush *Schoenoplectus tabernaemontani*, (C. C. Gmel.) Palla, all of which are characterized by salt tolerance. Due to the influence of brackish water, the climax vegetation of the fen is *Phragmites* reed. Extensive late summer mowing is directed by the lower nature conservation authority for the maintenance of open meadows, reasoned unspecifically with habitat diversification und nature conservation. There is no link of the measure to requirements of a Natura 2000 habitat management.

Investigation of soils

To characterize the eight PT sites investigated in 2021 (Table 1), three soil samples were taken on 18/06/2022 from each of the sites and a reference site (shore of creek Radelbach without Baltic Sea or salt influence) using a soil sampling cylinder (Ø 51 mm, height 54 mm). The following parameters were determined according to standard methods (VDLUFA 1991). The wet bulk density was determined gravimetrically. To determine the dry matter (DM), the total fresh matter (FM) was dried for 48 h at 105 °C and the dry bulk density and water content were calculated. The organic content was determined as loss on ignition at 550 °C and the carbonate content at 950 °C (3 h in each case). The salt content was determined via the electrical conductivity (KCl, nominal 25 °C).

Statistics (correlation analysis)

The Spearman rank correlation coefficient and Pearson correlation coefficient were used to test for correlation between different soil parameters and between soil parameters and activity densities of the investigated species. P-values were calculated to test for significance of the correlation, a significance level $\alpha = 0.05$ was applied.

Preparation, identification and storage of the material

The beetles from the PT were soaked in tap water with a few droplets of vinegar (70 %) for at least eight hours. All ind. were genitally prepared on moist filter paper, the aedeagus of the males was embedded in 40 % polyvinylpyrrolidone (Lompe 1986). The beetles were examined with an Olympus SZX10 stereomicroscope at a magnification of 4.7-71.2 ×. For the identification of the *Tychus* species the key of Besuchet (1974) and the illustrations of Hansen (1986) were used. The specimens are in the collection of the first author, two specimens each of *T. normandi* and *T. monilicornis* in that of Michael Schülke (Berlin) and Hannes Hoffmann (Hamburg).

Calculation of activity density

The 14d activity density (ADI_{14d}) for each species, emptying intervall and PTS was calculated from the number (n) of recorded individuals (ind.) per number (n) of functional PT on the basis of the 14-day PT intervals. It thus corresponds to the mean ADI_{14d} (number of ind./trap) across the PTS. Prolonged or shortened PT intervalls are considered with a correction factor for the number of active trapping days (d):

$$ADI_{14d,\, sp.\, i} = \frac{n(ind)}{n(PT)} * \frac{14d}{n(d)} \qquad (1)$$

The annual activity density (ADI) is given as the sum of ADI_{14d} over the entire trapping period, assuming that the study period (April to October) covers the whole main activity period of the investigated species. When the criterion of full coverage is met, annual sums can be used for interannual comparison:

$$ADI = \sum_{sampling\ intervall\ i\ =\ 1}^{n} ADI_{14d} \quad (2)$$

Calculation of catch continuity

The catch continuity (CC) was calculated as the percentage of sampling intervals (SI) within the study period with records of a certain species:

$$CC = \frac{n(SI\ with\ species\ records)}{n(all\ SI)} * 100\ \% \quad (3)$$

RESULTS

Species inventory Staphylinidae

In 2020, 4405 ind. of Staphylinidae (excl. Silphinae) were caught at the six PT sites and 171 species were recorded. These included 10 species of Pselaphinae (599 ind., 13.6 %) with 131 ind. *Tychus normandi* (21.9 %) and 15 ind. *T. monilicornis* (2.5 %). In 2021, 4842 ind. of Staphylinidae (excl. Silphinae) were caught at eight PT sites and 143 species were recorded. These included nine species of Pselaphinae (465 ind., 9.6 %) with 195 ind. *Tychus normandi* (41.9 %) and 23 ind. *T. monilicornis* (4.9 %). Thus, *T. normandi* was unusually much more common here than the otherwise numerically dominant species *Fagniezia impressa* (Panzer, 1805) (23.7 %) and *Rybaxis longicornis* (Leach, 1817) (20.0 %).

Habitat requirements of Pselaphinae

The following species of Pselaphinae were recorded in 2020 and 2021: *Euplectus nanus* (Reichenbach, 1816), *Bibloplectus ambiguus* (Reichenbach, 1825), *B. tenebrosus* (Reitter, 1880), *Brachygluta fossulata* (Reichenbach, 1816), *Fagniezia impressa* (Panzer, 1805), *Reichenbachia juncorum* (Leach, 1817), *Rybaxis longicornis* (Leach, 1817), *Bryaxis bulbifer* (Reichenbach, 1816) and *Pselaphus heisei* Herbst, 1791. Their coocurrence suggests overlapping habitat requirements across the pselaphine beetles. All nine species, including *Tychus normandi* and *T. monilicornis*, are hygrophilous and mostly paludicolous (Besuchet 1974, Koch 1989). *Tychus niger* (Paykull, 1800), a more common species in M-V, could not be detected in either year, even though a potentially suitable wet oak-alder forest site adjacent to the open fen (PTS OAF Tab. 1), investigated in 2020. The possible occurrence of *T. niger* (Paykull, 1800) in the NHH as a likewise hygrophilous but silvicolous species (Koch 1989) would have to be checked by including further forest sites adjacent to the open areas of the fen (Fig. 1).

Catch continuity of *Tychus normandi* and *T. monilicornis*

In contrast to *Tychus monilicornis*, *T. normandi* was detected at all investigated PT sites in the NHH in both years. The CC of both species was significantly higher in 2020 than in 2021 (Fig. 2), although significantly fewer captured individuals were taken into account. This strongly indicates a prolonged activity period of the imagines in 2020 compared to 2021.

In both years, the highest CC of both species (69.2 % and 38.5 % respectively) was achieved in the pristine, near-natural part of the fen in the climax reedbeds. *T. normandi* was caught with a higher CC over the course of the year at all sites, which might partly be explained by the overall higher ADI of *T. normandi* compared to *T. monilicornis.*

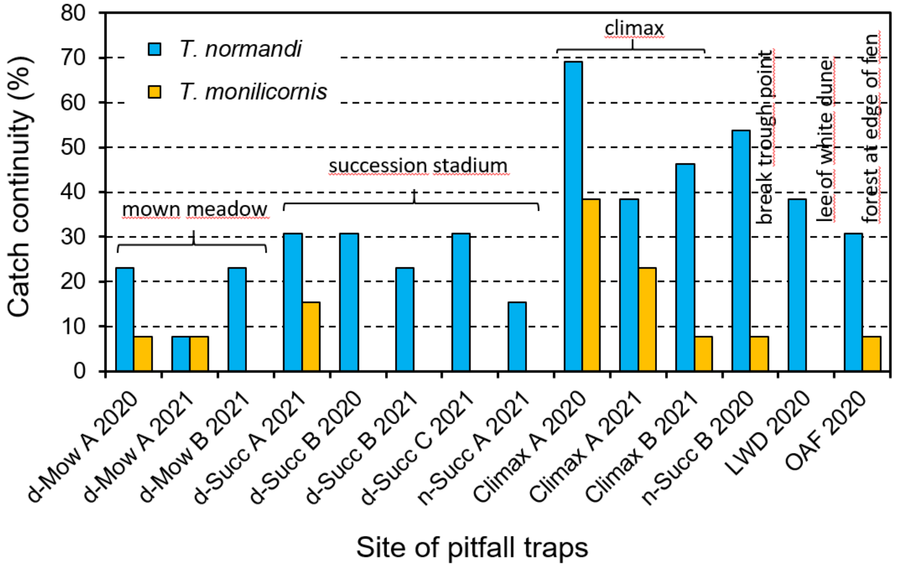

Fig. 2: Catch continuity (proportion of sampling intervals with species record) of *Tychus normandi* and *T. monilicornis* in the 'Heiligensee and Hütelmoor' nature reserve (Rostock, Mecklenburg-Western Pomerania, Germany) in the study periods 2020 and 2021.

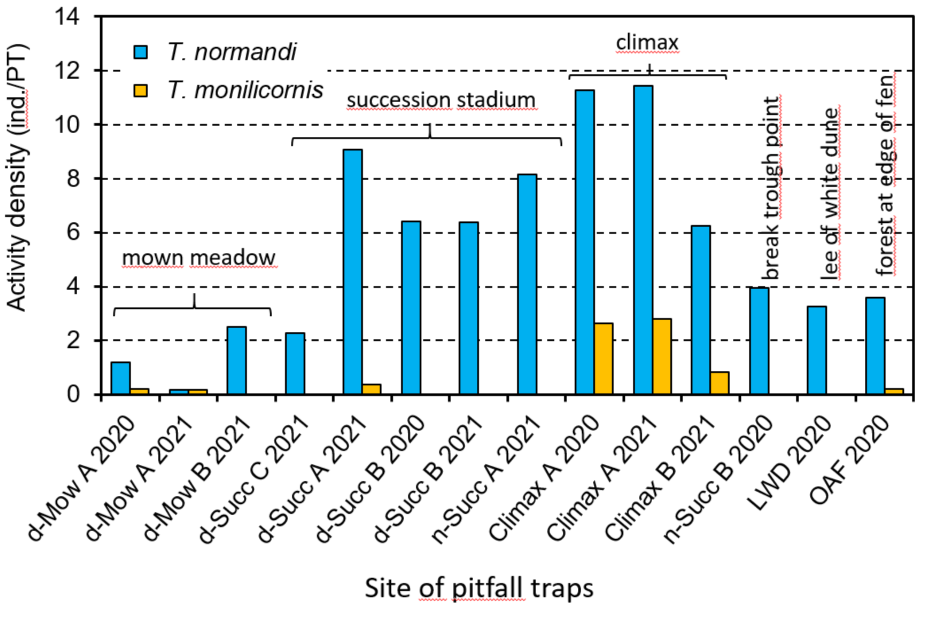

Fig. 3: Annual activity density sum ADI (individuals / pitfall trap, PT) of *Tychus normandi* and *T. monilicornis* in the 'Heiligensee and Hütelmoor' nature reserve in the study periods 2020 und 2021.

Activity density

The highest ADI for *Tychus normandi* was recorded in the wet successional and climax *Phragmites* reedbeds (Fig. 3). In contrast, the mown wet meadows and the fallow PTS d-Succ C had the lowest ADI. The species was also detected on the storm surge break trough point with oversanded peat at Lake Heiligensee, the lee of the white dune and in the wet forest at the edge of the fen. The ADI of *T. monilicornis* also indicates a clear preference for the climax reedbed (PTS Climax A) in the near-natural part of the coastal fen (Fig. 1). The high ADI of both species in both study years is remarkable.

In both years, the species were caught in a relatively constant ratio to each other. *Tychus normandi* had an annual average ADI of around nine times higher than *T. monilicornis* across all sites.

Seasonal occurrence (phenology)

In 2020, the activity peak for *T. normandi* was in the second half of May, for *T. monilicornis* between mid-May and mid-June. In 2021, the activity peak for *T. normandi* was in the first half of June, for *T. monilicornis* in the second half of June. Both *Tychus* species showed a significantly higher ADI_{14d} between the end of May and the end of June in both years. This corresponds to the time of reproduction of the imagines from the previous year. The activity in the late summer is interrupted probably before the new generation hatches, presumably between late August and early September. The second activity phase with only very low ADI_{14d} could indicate that the hatched animals immediately migrate to their winter habitats.

Apart from mid-August, *T. normandi* was detected throughout the entire study period 2020. The activity in the wet reedbeds started earlier and lasted longer than in 2021. Sites on the edge of the fen included in 2020 could serve as hibernation habitats. In the lee of the white dune, the activity peak of *T. normandi* precedes the main activity of the species in the fen, the last detection of the species was also in the lee of the dune at the end of October.

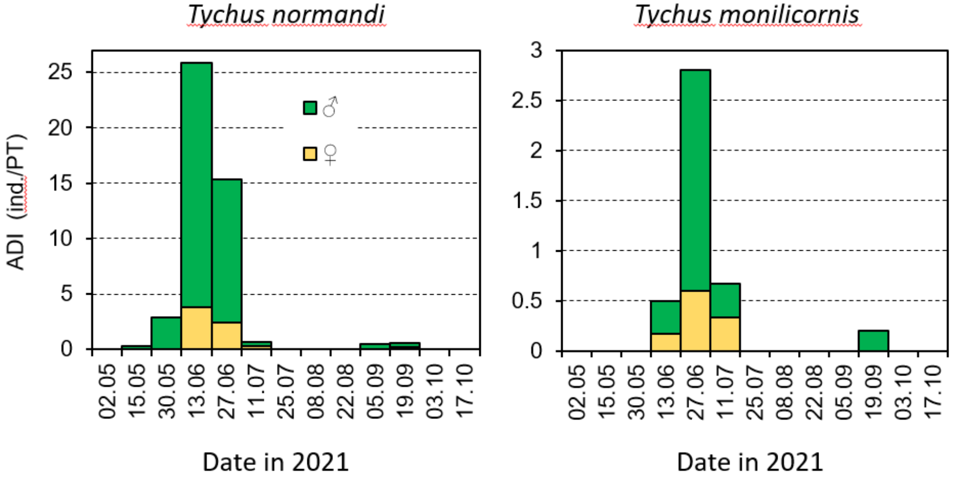

Fig. 4: Summed activity density (ADI, i.e. individuals/pitfall trap, PT) of *Tychus normandi* and *T. monilicornis* in the 'Heiligensee and Hütelmoor' nature reserve. The sum of the 14d activity density ADI_{14d} of males and females across all sites in 2021 is shown. Be aware of the different scale of y-axis.

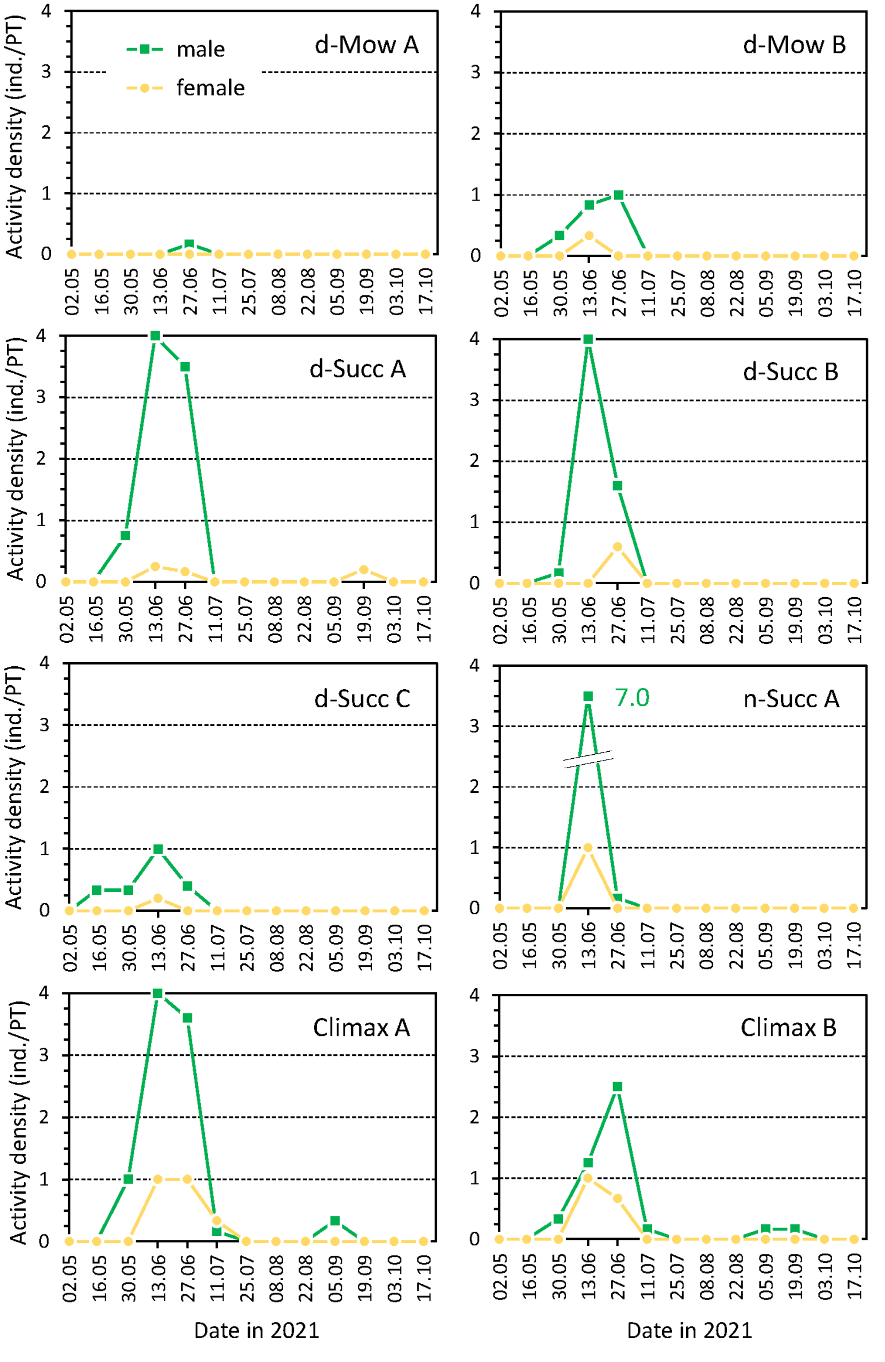

Fig. 5: Annual occurrence of *Tychus normandi* in the 'Heiligensee and Hütelmoor' nature reserve. The 14d activity density ADI_{14d} (individuals/pitfall trap, PT) of males and females at eight sites (see Tab. 1) in 2021 is shown.

For 2021, the seasonal occurrence was considered gender-specifically (Figs. 4, 5). The ♂ of *T. normandi* were already detected in early May, while the ♀ did appeared early June to early July. ♀ were also detected in the early fall peak. In case of *T. monilicornis*, ♀ and ♂ occurred simultaneously in early summer. The detectable activity phase of *T. monilicornis* was shorter than that of *T. normandi* in both years, which is probably due to the much lower density of individuals and the fact that the lower detection limit was probably reached more quickly. This might also apply to the detection of ♀ for both species before their activity peak, as their activity and probably also area density is much lower than that of the ♂.

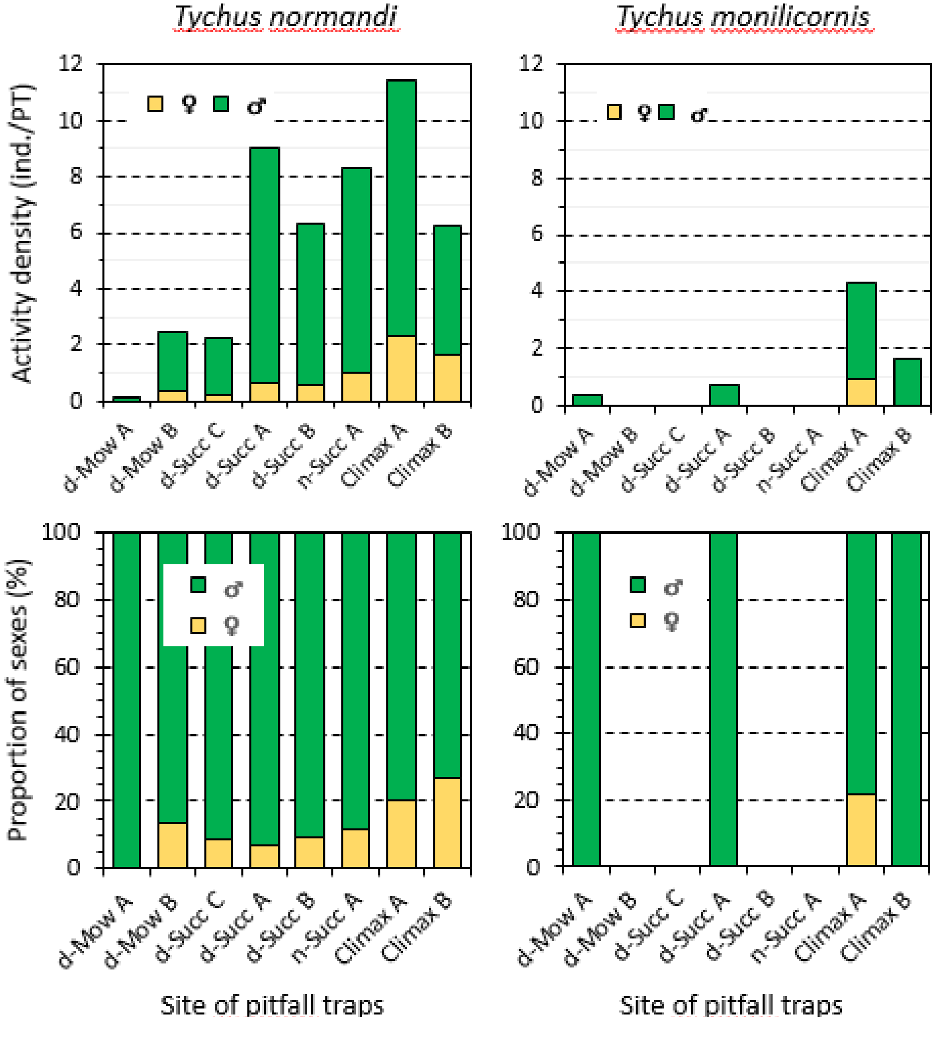

Fig. 6: Activity density (ADI, individuals / pitfall trap, PT) of females and males of *Tychus normandi* and *T. monilicornis* (upper panels), and proportion of the sexes of both species (lower panels) in the 'Heiligensee and Hütelmoor' nature reserve in the study period 2021.

Sex ratio

In 2021, most ♂ of both species were caught (Fig. 6). Of the 195 ind. *T. normandi*, 163 ♂ (83.6 %) and 32 ♀ (16.4 %) were caught, which corresponds to an average ♂ : ♀ ratio of 5.1. It remains unclear to which extend sex specific ADI differences result from differences in area density or sex specific activity patterns.
In case of *Tychus normandi*, an increase in the ADI of the ♀ is evident along the utilization gradient (Fig. 5). While the proportion of ♀ in the mown meadows and succession areas varies between 7 % and 13 %, it is between 20 % and 27 % in the climax reedbed areas. In the case of *T. monilicornis*, ♀ with a proportion of 22 % were only found in climax reedbed in the near natural part of the fen. On the climax sites (PTS Climax A and B), the ADI of the species is significantly higher than in the rewetted part of the fen, where only single ♂ were detected.

Tab. 2: Mean value and standard deviation (in brackets, n = 3) of pedological parameters of the pitfall trap sites in 2021 in the 'Heiligensee and Hütelmoor' nature reserve compared to a reference site (Ref.) that was not influenced by the Baltic Sea. Soil cores were taken at the 18th of June 2022, in the phenological activity peak of the *Tychus* species. Abbrevations: FM = fresh mass, DM = dry mass, KCl = potassium chloride.

Pitfall	Bulk den-	Dry bulk	Dry	Water	Loss on ignition		Salt content
trap	sity (wet)	density	mass	content	550°C	950°C	KCl
Site	[mg/cm^3]	[g/cm^3]	[% FM]	[% FM]	[% DM]	[% DM]	[mg/100 g DM]
d-Succ A	1.39	0.65	45.9	54.1	15.4	0.33	74.8
	(0.04)	(0.11)	(5.1)	(5.1)	(2.8)	(0.01)	(4.6)
d-Mow A	1.21	0.29	23.7	76.3	71.1	0.68	143.0
	(0.02)	(0.03)	(2.4)	(2.4)	(2.5)	(0.05)	(22.2)
d-Succ B	1.77	0.53	37.8	62.2	24.2	0.61	214.1
	(0.58)	(0.15)	(7.4)	(7.4)	(0.3)	(0.06)	(24.7)
d-Mow B	1.25	0.17	17.9	82.1	79.3	0.81	286.4
	(0.56)	(0.04)	(3.9)	(3.9)	(6.0)	(0.02)	(38.8)
d-Succ C	1.48	0.43	32.6	67.4	36.3	0.48	108.6
	(0.61)	(0.25)	(13.2)	(13.2)	(1.3)	(0.03)	(14.9)
Climax A	1.11	0.16	14.4	85.6	72.0	1.28	340.3
	(0.03)	(0.02)	(1.2)	(1.2)	(3.2)	(0.01)	(32.5)
n-Succ A	1.10	0.15	13.0	87.0	76.3	1.24	867.4
	(0.08)	(0.01)	(0.2)	(0.2)	(3.9)	(0.05)	(57.8)
Climax B	1.11	0.27	23.8	76.2	48.6	0.93	548.0
	(0.18)	(0.07)	(3.0)	(3.0)	(7.7)	(0.10)	(23.0)
Ref.	1.53	0.89	58.0	42.0	12.3	0.85	85.1
	(0.07)	(0.07)	(2.0)	(2.0)	(1.5)	(0.03)	(6.1)

Salt preference of *Tychus normandi* and *T. monilicornis*

To examine a possible influence of salt on the occurrence of both species, the eight PT sites (Tab. 1) investigated in 2021 were pedologically characterized in comparison to a reference site unaffected by the Baltic Sea and the salinity was determined (Tab. 2).

The NHH soils sampled had a low bulk and dry density. Corresponding to the high water content of the soil at the time of sampling, the proportion of DM was also proportionally low. A positive non-linear relationship was found between the loss on ignition (550 °) and the water content (Tab. 2) [power regression formula: $y = 0.0002x^{2.8781}$, $R^2 = 0.9105$; n = 8, Spearman correlation: 0.95, p = 0,00035 (***)]. From the PT site d-Succ A to the PT sites n-Succ A and Climax B (Fig. 1), a salt gradient was observed for the calcareous soils. The PT site n-Succ A had a salinity 10 times higher than the reference site, which was not influenced by the Baltic Sea.
A habitat preference of both *Tychus* species with regard to conductivity or salinity (Tab. 2) could not be detected. No correlation was found for halophilic species such as *Philonthus salinus* Kiesenwetter, 1844. In contrast, a significant correlation between salt content and ADI was found for *Quedius balticus* Korge, 1960 [n = 8, Pearson correlation: 0.8849683, R^2: 0.7831688, p = 0.0035(**)], which is common in the NHH.

DISCUSSION

Geographic distribution and habitat preference of *Tychus normandi* and *T. monilicornis*

The individual-rich occurrence of both species in the coastal fen NHH is remarkable. *Tychus normandi* and *T. monilicornis* are extremely rare in Germany and threatened with extinction (Schmidl et al. 2021). Like all species of Pselaphinae recorded in the NHH, both species are hygrophilous (Koch 1989). Accordingly, they preferentially colonize moist to wet sites, in the NHH preferably the *Phragmites* reedbed PTS d-Succ A and the reedbeds near Lake Heiligensee (PTS Climax A, n-Succ A and Climax B, Tab. 1, Fig. 1). Especially in the near-natural part of the fen, both *Tychus* species, but above all *T. normandi*, were detected in a broader range of habitats with a high CC (Fig. 2) and ADI (Fig. 3, 5).

The species are widespread across Europe. Several records from Sweden suggest that both species are not closely tied to certain biotopes (Sörensson 1983). Biotope descriptions here highlight the occurrence in open eutrophic wetlands, which probably refers to dense reedbeds. All the records in Germany were made in open eutrophic fens or swamps, rather matching the predominant records in open wetlands made in Sweden. In M-V, up to now, there have only been records in *Phragmites* reedbeds in coastal fens (Kleeberg 2023).

In contrast, all Danish individuals for which detailed records are available were caught in deciduous forests on marshy ground, especially in alder swamps (Hansen 1986). They were found under foliage or in moss, i.e. preferably at the base of trees or bulbs of sedges (Hansen 1986). In the Czech Republic, *T. normandi* was caught in wet leaf litter at the edge of temporary water bodies in swamps and riparian forests (Šíma et al. 2018). Wooded marshes, swamps and margins ponds and lakes appear to be the common biotopes for the species also in their southern areal (e.g., Vincent 2022, Sabella & Šíma 2016)

In the north-eastern areal boundaries, the species apparently occurs more frequently in open wetlands in the proximity of the coast.

These might be more favourable reproductive habitats due to the significantly warmer mesoclimate (forest canopies significantly reduced summer temperatures (Haesen et al. 2021)) and additionally the more moderate maritime macroclimate. A potential peripheral biotope preference shift, as it apparently occurs in the north, might help to meet the thermal requirements of the species probably adapted to rather warmer oceanic climate.

Seasonal occurrence and natural spatial dynamics

Tychus normandi and *T. monilicornis* were mainly caught from the end of May to the end of June and again in smaller numbers in September (Figs. 4, 5). Further records would be possible in the NHH using sweep nets, as the *Tychus* species tend to show swarming behaviour towards evening (Hansen 1986).

Both species overwinter as imago; *T. normandi* was found in Sweden in early September as a freshly hatched imago (Sörensson 1983). In the NHH, imagines were found in late August/early September 2021, which presumably belonged to the new generation. The fall activity of the two *Tychus* species was hardly detectable in 2020 and 2021, which hints toward an immediate migration of the freshly hatched imagines to the winter habitats. The weather conditions in the NHH that generate storm floods or flooding due to excess water are usually limited to the winter half-year (Selle et al. 2016). During this time, *Tychus* species migrate to less humid habitats than those in which they reside during the active period (Hansen 1986). Their life cycle is thus optimally adapted for life in winter-flooded areas. The activity observed in 2020 in the lee of the white dune before the activity peak on the peatland sites and at the end of the season could indicate that *T. normandi* also hibernates in the immediate vicinity of the dune dyke, which offers protection from the winter flooding of the peatland areas. The activity peak in the wet forest at the edge of the fen (Fig. 1), on the other hand, overlaps in time with the open biotopes of the fen, but is comparatively low. Based on the activity patterns, it probably belongs more to the reproductive habitat of the species.

The differences in seasonal occurrence in 2020 and 2021 are probably due to the weather conditions. In 2020, a mild, sunny spring with little precipitation caused water to recede more quickly in the fen, allowing activity to begin earlier in the temporarily flooded sites. The summer was rather cool, which prolonged the activity of both species in the summer months. In 2021, the cooler spring with high precipitation and the warmer summer with less precipitation led to a compression of the main activity phase of both species. The activity peak (ADI_{14d}) was recorded two weeks later than in the previous year. This result is well substantiated, as the ADI of the two species in reedbed PTS Climax A was almost identical in both years. Thus, both *Tychus* species show a certain degree of phenological plasticity in response to unfavourable conditions.

Sex ratio

The ratio of ♂ to ♀ indicates that the ♂ of both *Tychus* species are significantly more active during the main activity period (Figs. 4-6), probably in search for ♀. It seems that sex ratio is influenced by the land use history. The highest number of ♀ of both species was recorded in pristine climate reedbeds that haven't been in agricultural use for at least 70 years. For *T. monilicornis*, ♀ were only recorded there, ♂ appeared here in relevant numbers, in contrast to other sites where only single ♂ were recorded. The presence and ADI of ♀ is a more reliable indicator of suitable habitat conditions compared to the ♂, which might occur in a wider range of sites in search for ♀. For *T. normandi* ADI of ♀ and ♂ was lowest on the mown wet meadows and increased with the degree of naturality.

Salinity preference

As anticipated, a salinity gradient was observed in the NHH (Tab. 2), i.e. from the PTS d-Succ A far from the Baltic Sea to the PTS n-Succ A and Climax B close to the Baltic Sea (Fig. 1). The soil was sampled during the reproductive phase (activity peak) of both *Tychus* species, when the females seek for the optimal habitats. A salt preference should then probably be most likely to detect. Nevertheless, no correlation between the salinity gradient and the activity density of the *Tychus* species was found. All Pselaphinae recorded in the NHH occur in low-salinity environments, i.e. they appear to be halotolerant. Maybe some of them are weak competitors and are therefore displaced into saline habitats (Wolender & Zych 2007, Irmler & Lipkow 2018). The distribution of *Tychus* species in the NHH (Fig. 3) shows that they are able to adapt to or evade the prevailing higher, rather moderate salinity levels (Tab. 2) in the short or long term. Because of their presence in the brackish reedbeds of the NHH, it is reasonable to assume that their physiology allows them to colonise thalassohaline (NaCl) sites, provided these do not dry out too much.

The only positive correlation between abundance and conductivity found for *Quedius balticus* (eurytopic), is not necessarily to be interpreted as a causal relationship of salt preference, but rather a preference of the species with regard to the water supply of the sites. The species is paludicolous, phytodetriticolous and hygrophilous (Koch 1989). In analogy to the two *Tychus* species (Fig. 2), the highest numbers of individuals of *Quedius balticus* were determined at the moist to wet *Phragmites* reeds (PTS n-Succ A, Climax A and B (Fig. 1). For the halophilic, simultaneously ripicolous *Philonthus salinus*, a salt dependence was not detectable, maybe masked by the habitat preference sand.

There are numerous limitations and difficulties in assessing salt preference. The NHH is geohydrologically very heterogeneous, i.e. in terms of soils, thickness and conductivity of the layers, type of peat and its degradation as well as the microrelief (Selle et al. 2016, Miegel et al. 2016, 2017). The heterogeneity of the soils sampled once (Tab. 2) makes it difficult to assess salt dependence, not only of the *Tychus* species. Most important, the salinity gradient is subject to changes in seasonal course in particular due to possible salt water influx, but also depending on a complex interaction of precipitation, drainage, soil hydrology and evapo-transpiration and other factors. Further long-term investigations would be required to understand spatio-temporal variations in top-soil salinity of the NHH in detail, which is influencing the arthropod communities.

Water supply of the fen and the *Phragmites* reed beds

Crucial is the episodic and sufficient water supply of the reed beds (low water level gradients, hydraulic resistance of the vegetation, strongly attenuated area runoff, cf. Miegel et al. 2016), which provides optimal habitat conditions for the *Tychus* species. Both species were caught in the NHH, particularly in eutrophic fens with *Phragmites australis* (Tab. 1, Figs. 2, 3, 5). Around 70 % (formerly 237 ha, Dahms 1991) of the lowlands are occupied by reeds (Miegel et al. 2016). Such brackish water reedbeds represent the potential natural climax vegetation of recent coastal flooded marshes (Kopp et al. 2005). Reed favours fluctuating water levels; stable water levels can lead to its decline. Under oligo- to mesohaline brackish water conditions, *P. australis* in particular outcompetes the light-demanding halophytes of salt marshes (Jeschke 1987, Kopp et al. 2005). Moderate salt stress (Tab. 2) is tolerated, higher salt stress hinders its growth (Mal & Narine 2004). Reeds grow on soils with very different organic contents (1-97 %, Mal & Narine 2004). The higher organic content of soils in the NHH (Tab. 2) favours water retention and reduces the risk of drying out too quickly.

Due to the groundwater close to the ground, the reedbeds in the NHH are classified as optimally supplied with water (Miegel et al. 2016, Schreiber et al. 2021). With their year-round vegetation height >2 m (Tab. 1), the reedbeds provide a distinct microclimate. The stands favour subdued air temperatures but also very high transpiration rates (Mal & Narine 2004, Dietrich et al. 2019), despite individual patches of low vegetation. In general, reedbeds reach their maximum transpiration rate in summer with rates of 5-13 l m^{-2} (Mal & Narine 2004), i.e. almost at the same time as the highest abundances and ADI of both *Tychus* species (Fig. 3-6). Water level and vegetation height have an influence on the abundance of staphylinids (Hoffmann et al. 2016).

Under north-east German climatic conditions, water loss through evaporation is usually greater than the water supply from precipitation; in dry years, it is often more than twice as high (Dietrich et al. 2019). Evaporation also dominates in late spring and summer, causing water levels to fall (Miegel et al. 2016). At higher air temperatures and simultaneously lower humidity, water loss increases, especially affecting larvae (high cuticular permeability) and imagines of the Staphylinidae (Whitehead 2006, Bong et al. 2013). The deficit in the climatic-hydrological balance reveals the dependence of the lowland area NHH on the inflows from the catchment area (Miegel et al. 2016, 2017) and thus the dependence of the hygrophilous arthropod communities, including both *Tychus* species, from a continuously sufficient water supply. A combination of climate change, altered precipitation patterns and the drainage of the catchment area might negatively affect the water balance of the fen. Water retention in the catchment areas especially in the precipitation rich winter half year and in the fen in the summer half year will gain importance in the future to maintain a sufficient water supply of the peatland and to protect its special fauna.

Influence of mowing on site and habitat conditions

The diversity of soils with decaying plant remains of the litter layer, humus and moss forms a small-scale mosaic of moist habitat structures that provides the necessary resources (e.g. mites) for the predatory Pselaphinae (Besuchet 1974, Schomann et al. 2008). A low bulk and dry density (Tab. 2) indicates a correspondingly large pore volume. The extensive gap system of the topsoil and the litter layer, which is created during undisturbed soil formation, not only ensures a high water storage capacity during precipitation events, but is also the habitat of springtails and mites, which serve as food for the Pselaphinae. The compaction of this pore space by heavy agricultural machinery during mowing leads to a decline in soil microfauna (Dittmer & Schrader 2000, Lübke-Al Hussein et al. 2008) and thus also to a decline in available food resources for the pselaphine beetles. The compaction of the topsoil reduces the water storage capacity of the pore space and increases the probability of drying out in summer. Mowing also leads to a strong reduction in the litter layer by reducing above ground plant biomass, which is an obligatory habitat feature for the Pselaphinae. This is presumably mainly due to the damp, cold and shady microclimate in the litter layer and the protection of the topsoil from drying out.

The ratio of ♂ to ♀ suggests that in both *Tychus* species, the ♂ are significantly more mobile and active, especially during the main activity period (Fig. 5), probably in search for ♀. The ♀ that do occur, on the other hand, are likely concentrated in habitats with optimal conditions for reproduction. It is therefore not surprising, that the proportion of ♀ increases with the degree of naturalness of the sites (Fig. 6). The mown grassland probably has only a low habitat suitability for the *Tychus* species, which is reflected in the lower CC (Fig. 2) and ADI (Fig. 3). The significantly higher ADI of *T. normandi* on the reference area d-Succ A in 2021 compared to the mown grassland d-Mow A in 2021 is striking (Fig. 3). The number of individuals of other species, such as *Quedius balticus*, also increased from the disturbed to the intact sites (Fig. 6). Mowing is undoubtedly one of the stressors of cenoses with negative effects, especially on their developmental stages and habitat suitability for rare and endangered species of wet grassland and reedbeds (Lindner et al. 2025).

CONCLUSIONS

The occurrence of the two extremely rare pselaphine beetles *Tychus normandi* and *T. monilicornis*, which are threatened with extinction in Germany, exemplary illustrates the special role of intact, unutilised brackish reedbeds for species conservation. At the same time, it highlights the complexity of the interacting factors in natural areas that influence the occurrence and conservation of highly specialized arthropod species. Only a sufficient water supply from precipitation, surface and subsurface inflow from the catchment area or episodic Baltic Sea water ingress can secure the populations of hygrophilous communities of rove beetles in reed beds, and thus those of the *Tychus* species. These species can avoid winter storm surges and temporary flooding by seeking out higher lowland areas as winter habitats. The relatively rapid superficial dilution after saltwater intrusions reduces possible salt stress for the halotolerant *Tychus* species. Due to their phenological plasticity they can adjust to the natural water level dynamics of their reproductive habitats caused by weather variations. Possible summer habitat shifts from wet forest to open reedbeds in the northeastern areal margins might help the species to cope with the suboptimal climatic conditions. Anyway, these species will have to cope with changing habitat conditions in near future, caused by climate change, especially changes in regional precipation patterns and sea level rise, e.g. by migrating to areas with an adequate water supply. Grassland management i.e. of areas of a designated NPA, is subject to the requirements of biodiversity conservation. Further research on the effects of salt grassland management on soil arthropod communities is required. The results from the NHH (Lindner et al. 2025), hint on a conflict between the management and the conservation of rare and threatened ground Arthropods, as the *Tychus* species. Wilderness concepts for the restoration and protection of self-adapting and self-stabilizing wetland ecosystems will become increasingly important under the impact of a rapid climate change and sea level rise. The disjunct and exclusive distribution of the here discussed species highlights the exceptional importance of large protected wetlands with a high natural landscape dynamic as the NHH.

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