SHORT COMMUNICATION

Differentiation of activity rhythms and space use between two competing water shrew species in a laboratory experiment

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Abstract

Hypotheses about the differentiation of activity rhythms and space use between two competing species of water shrews, *Neomys anomalus* [AA] and *N. fodiens* [FF], were verified in a laboratory experiment. The animals were kept together for 2 months in an enclosure (195 × 145 cm) and their activity was video recorded using the time-lapse mode. Changes in activity rhythms, distances kept between active animals, and frequency of interspecific conflicts were compared between the early (first 24 h) and late (last 24 h, after 2 months) phases of the animals' coexistence in the mixed group. In both phases, the activity of both species was relatively evenly distributed over 24 h, with breaks in activity nearly every 1 h. During the early phase, both species were equally and simultaneously active, whereas in the late phase, as predicted, the activity of FF was lower than that of AA, and asynchronous. In the late phase, pairs of different species (F-A) were rarely active simultaneously and kept long inter-individual distances. Consequently, the number of conflicts decreased. The results suggest that, over time, water shrews can develop mechanisms diminishing interference competition, which are based on shifts in activity rhythms, maintaining distance between individuals, and the rare usage of the same shelters and feeding sites.

Keywords Circadian activity · Interspecific competition · Conflict avoidance · Temporal niche · Keeping distance · Soricidae

Introduction

Interspecific competition, resulting from the use of the same limited environmental resources, is one of the most important ecological interactions and forces driving evolution (Begon et al. 2006; Krebs 2009). Therefore, there is still a need to investigate mechanisms that allow the coexistence of ecologically similar species. One of the reasons is that with this knowledge, we can better manage and protect rare species and threatened populations.

Long-term stable coexistence of two or more species is possible if their ecological niches differ sufficiently in at least one dimension (Schoener 1974; Begon et al. 2006). These dimensions include the type of food, habitat, and time of activity (Schoener 1974; Rychlik 2004). Separation of temporal niches is an important mechanism for diminishing competition and allowing the coexistence of mammal species forming guilds (Schoener 1974; Halle 2000; Rychlik 2005). This has been recently demonstrated for some carnivores from different regions (Rasphone et al. 2020; Tsunoda et al. 2020; Ferreiro-Arias et al. 2021; Vernes et al. 2022). Among small mammals, the separation of temporal niches among many rodent species has been proved before (Kotler et al. 1993; Kronfeld-Schor and Dayan 1999; Ziv and Smallwood 2000; Castro-Arellano and Lacher 2009).

However, the situation with shrews (Soricidae) is not so obvious. Due to a very high metabolic rate and energy needs, shrews display a high level of activity and polyphasic activity rhythms (Hanski 1985; Saarikko and Hanski 1990; Merritt and Vessey 2000). Moreover, common phylogeny constrains the ability to considerably differentiate temporal niches between closely related species (Roll et al. 2006; Hut et al. 2012). Therefore, it is generally difficult to identify clear interspecies differences in the activity time of

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coexisting shrews (Castién and Gosálbez 1999; Merritt and Vessey 2000; Rychlik 2005). Consequently, there is no direct evidence (neither from observations in nature nor from laboratory tests) showing that the different patterns of circadian activity among shrew species or changes in these patterns are due to interspecific competitive interactions (Merritt and Vessey 2000; Rychlik 2005).

Nevertheless, theoretical models predict that (i) temporal partitioning may facilitate the coexistence of competitors, (ii) circadian rhythmicity allows for the differentiation of temporal niches, and (iii) two competing species that are initially active in the same phase, will differentiate their rhythms (shift their phases) enables them to coexist infinitely (Kronfeld-Schor and Dayan 2003; Gao et al. 2020). That is because temporal partitioning may lead to the avoidance of confrontation and interference competition (Kronfeld-Schor and Dayan 2003). Surprisingly, studies demonstrating temporal shifts induced by competition or plasticity in circadian activity are rare (Kronfeld-Schor and Dayan 2003). However, such works have recently appeared (e.g., Cohen et al. 2009; Harrington et al. 2009; Monterroso et al. 2014), although they did not study shrews. Therefore, we wanted to check whether such a competition-induced shift of activity rhythms could occur in shrews. We decided to do it experimentally because experimental data are the most compelling in testing such predictions (Kronfeld-Schor and Dayan 2003).

The circadian activity of two water shrew species, the Mediterranean water shrew *Neomys anomalus* Cabrera, 1907 and the Eurasian water shrew *N. fodiens* (Pennant, 1771) [denoted as AA and FF, respectively], was analyzed in the wild in Białowieża Forest (Rychlik et al. 2004; Rychlik 2005). Investigating circadian activity through continuous live-trapping and controlling trap 5 times a day, Rychlik (2005) found that both *Neomys* species displayed very similar (nocturnal and unimodal) patterns of activity, and their temporal niches overlapped in 99.29%. However, Rychlik et al. (2004) found that experimental introduction or removal of the dominant FF caused shifts in microhabitat selection and circadian activity of subordinate AA. Therefore, we hypothesize that differences in activity rhythms on a rather fine scale could contribute to a separation of their ecological niches. Moreover, if the differentiation of activity patterns is to be an efficient mechanism for diminishing interspecific competition, it must be assumed that the activity patterns of individual species are not constant over time, but they can be modified (adapted to the current situation), especially by the subordinate competitors. Thus, the main aim of this study (based on long-term observations) was to verify the hypothesis (H1) that over time, the activity rhythms of AA and FF will differentiate, i.e., become asynchronous as predicted by the models of Gao et al. (2020). Such a divergence of activity peaks would allow them to reduce the number

of interspecific conflicts. The other objectives were the following:

(1) To describe patterns of circadian activity of the two water shrew species under laboratory conditions and to compare changes in their activity between the early phase (first 24 h) and the late phase (last 24 h, after 2 months) of coexistence in a mixed group. These species differ in body masses, metabolic rates, and food requirements—*N. anomalus*: BM (body mass) = 10.0 g, BMR (basal metabolic rate) = 4.98 ml O_2/(g h), M-SPU (mass-specific prey utilization) = 96.75 mg/(g h); *N. fodiens*: BM = 14.4 g, BMR = 3.61 ml O_2/(g h), M-SPU = 79.25 mg/(g h) (Vogel 1976; Taylor 1998; Rychlik and Jancewicz 2002). Energy reserves in adipose tissue are relatively greater in large shrew species than in small ones (Hanski 1985; Rychlik 2005). Consequently, the starvation time of large shrews and breaks in their feeding are longer than in small shrews (Hanski 1994). Therefore, *N. anomalus* (as the smaller species with a higher metabolic rate) was expected (hypothesis H2) to display a higher activity level, with activity bouts more equally distributed between day and night than *N. fodiens*.

(2) To estimate whether the distances kept between simultaneously active individuals were different between the species and if this difference could be associated with sociability and competitive interactions of the studied species. We assumed that (H3) AA individuals would stay more frequently at long distances from FF individuals than at short distances. This hypothesis is based on the observations that *N. fodiens* dominates *N. anomalus* (Rychlik and Zwolak 2006), and the number of conflicts with a dominating species decreases with an increase of distance between opponents (Rychlik and Zwolak 2005). It was expected that the distances kept between simultaneously active shrews would generally increase between the early and late phase of the experiment and that this increase would be greatest for interspecific pairs of individuals. We also expected that AA would tend to avoid nest boxes and feeding trays utilized by FF, which are more aggressive and dominant in conflicts near food and shelters (Krushinska and Rychlik 1993; Rychlik and Zwolak 2006).

Materials and methods

The procedures of this study followed those described by Krushinska and Rychlik (1993). Four individuals of FF (2 males and 2 females) and 4 AA (3 males and 1 female), captured in the Białowieża Primeval Forest (on two trapping plots separated by approx. 1 km) were used in the experiment. All 4 AAs and 2 FFs were trapped in the first plot, whereas 2 other FFs in the second plot. All shrews were subadult, i.e., fully grown (body mass over 9.5 g in AA and 14 g in FF) but sexually inactive. All animals underwent

at least a week of acclimatization in individual cages ($38 \times 30 \times 16$ cm). Additionally, all FF were marked with an orange plastic badge (4 mm in diameter), glued with a surgical adhesive to the top of their heads. Such marking allowed the species to be easily distinguished in video records.

Marked animals were introduced to a big enclosure (195×145 cm) built in the laboratory. Its floor was covered with a 5-cm layer of sand. A small amount of moss for nest-building was put on the sand and replaced every 2–3 weeks. Enclosures were also provided with 10 nest boxes (upturned clay flowerpots filled with moss), 5 feeding trays (on which food and drink containers were placed), and 1 water basin about dimensions $80 \times 25 \times 15$ cm (Fig. S1 in the 'Supplementary information'). Meat, milk, and water were given ad libitum according to Michalak's standard (1987). Natural light during the day and artificial red light during the night were used for observations. The mixed group of two water shrew species was established on 1st July 1991 and maintained for 2 months.

Activity and social behaviors displayed by water shrews were video recorded with a camera hanging over the enclosure. The video records from the early phase of the mixed group existence (01–02 July 1991; initial interactions between animals) and the late phase (27–28 August 1991; stabilized interactions) were analyzed. More specifically, the 5-min periods selected every half hour from the 24-h recording were analyzed. However, the 5-min periods were represented by 20 s of the recording because the time-lapse mode was set to record 1 s every 15-s interval. Due to breaks, or poor-quality recordings caused by technical problems, we were not able to analyze 14 of the 48 5-min periods from recordings of the early phase and 4 of the 48 periods from the late phase.

For every 5-min period, all animals visible outside nest boxes (i.e., active) and their behavior (like locomotor activity, feeding activity, visiting nests, social interactions) has been reported. The enclosure was divided into 12 squares (4 zones in 3 rows: A, B, C; Fig. S1) to determine the position of the individuals (i.e., entering or near a given nest box, near a given feeding tray, or in an open area of the enclosure) and to calculate the distance between animals. The distances between simultaneously active water shrews were also classified into four categories of 50-cm range: 0–50 cm = short distance, 51–100 cm = medium, 101–150 cm = long, and 151–200 cm = very long distance. Simultaneous activity of intra- and interspecific groups of animals was also noted.

The similarity of circadian activity rhythms was assessed by the Circular Data Correlation test, using the NCSS 2022 Statistical Software program (version 22.0.4, released 04.08.2022; NCSS, LLC. Kaysville, Utah, USA, ncss.com/software/ncss). Replicated goodness-of-fit tests (G-statistic) (Sokal and Rohlf 1995) were performed to compare the overall activity levels of the two species. Changes in the simultaneous activity of shrews and distances maintained between simultaneously active individuals were analyzed with generalized linear mixed models in R (R Core Team 2020) using package glmmTMB (Brooks et al. 2017). The activity was analyzed using binomial error family and logit link; the distance with Gaussian error family and identity link. In both models, fixed effects included phase (early vs. late), type of activity (two AA, two FF, or a mixed pair: FF-AA), and their interaction. The 5-min period was entered as a random effect. In addition, the model of activity was corrected for temporal autocorrelation (AR(1) covariance structure).

Results

Differentiation of activity rhythms and frequency of conflicts

During the early phase (first 24 h), 377 observations of active animals were registered. Of these, 184 were of FF and 193 of AA. Shrews from both species were active throughout the 24 h, only being inactive for short periods almost every hour (Fig. 1a). Short interruptions in the shrews' activity occurred most often simultaneously in both AA and FF, and only occasionally occurred alternately. The circadian rhythms of activity of both species practically coincided, as expected. The rhythms tended to correlate positively with each other, though the relationship was insignificant (Circular Data Correlation: correlation coefficient $r = 0.252$, the value of $Z = 1.387$, $p = 0.166$; Fig. 1c).

Simultaneous activity of shrews during the early phase resulted in five long-lasting and serious interspecific conflicts which were observed mainly during the first 6 h of recording: dominant individuals of FF expelled AA individuals from the nests (recorded twice), chased them away from feeding trays (recorded twice), and attacked in the free space of the enclosure (one such observation). In addition to these, we also observed several short and less serious conflicts (threats, jumps, leaps, and escapes), but recording videos in time-lapse mode made it impossible to accurately recognize and count them, so we did not attempt to present them as quantitative data.

In the late phase, active animals were observed 401 times within 24 h, of which 261 were AA and 140 were FF. Both species still alternated periods of their activity and rested frequently (every 30–90 min), but in most cases, the two species were not active simultaneously (Fig. 1b). Therefore, the rhythms of their activity did not coincide, and they significantly correlated negatively with each other (Circular Data Correlation: $r = -0.325$, $Z = -2.187$, $p = 0.029$; Fig. 1c). AA individuals usually reduced their activity or stayed in nest boxes when the dominant FFs were more

Fig. 1 Comparison of the circadian activity rhythms of the two water shrew species in the **a** early, and **b** late phases of their coexistence in an experimental enclosure. The activity was expressed as the number of observations of individuals of a given species during the 5-min period. **c** Plots illustrating the results of circular data correlation between activity rhythms of the two species in each phase. FF—*Neomys fodiens*, AA—*N. anomalus*
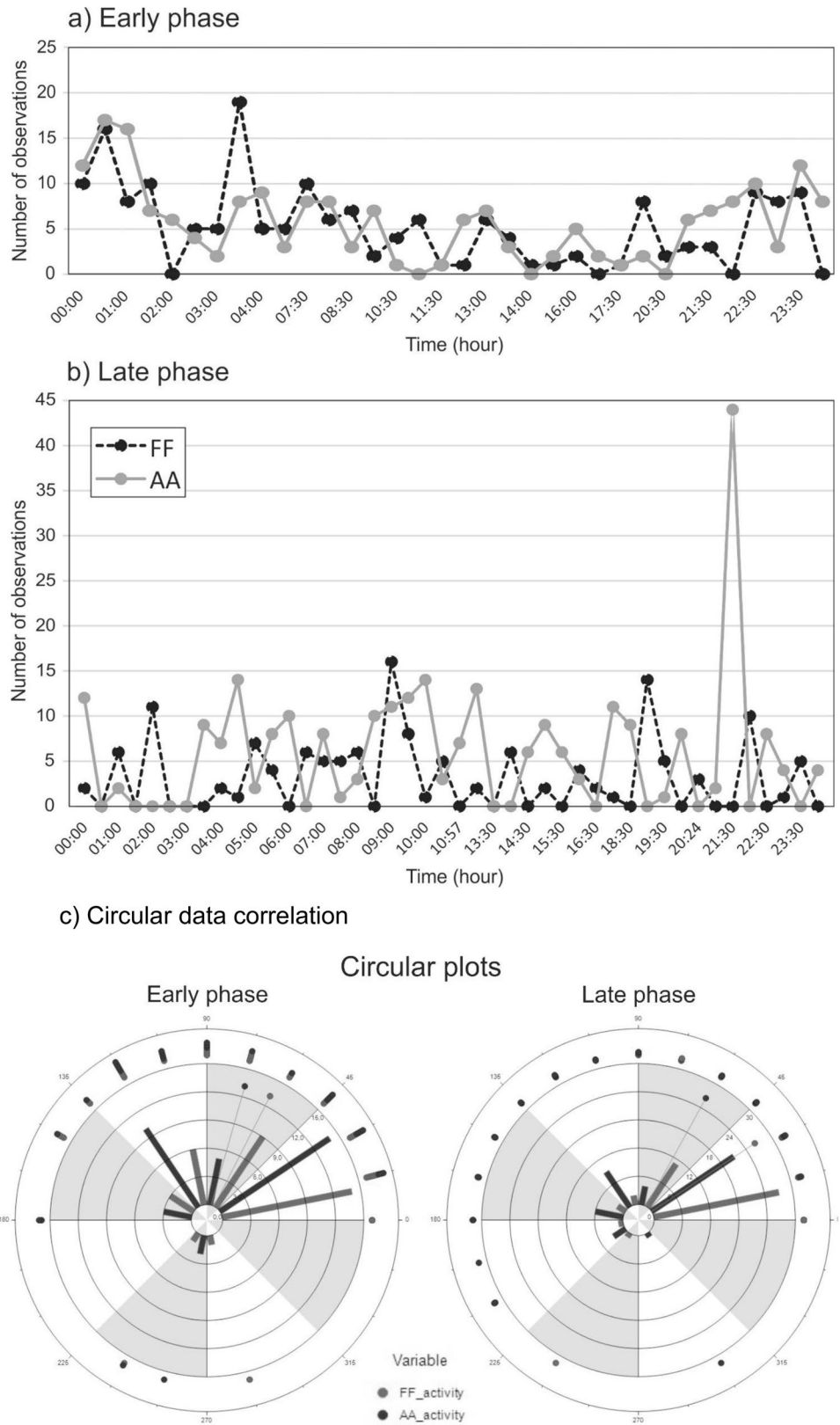
active. Nevertheless, in many instances, shrews of the two species were active at the same 5-min period; however, the

AA individuals usually kept a distance from FF shrews (see next section) and avoided contact. Thus, direct interspecific

conflicts (including attacks, jumping on, combats, and chases) or other signs of antagonism were not observed in this phase.

At 21:30, an enormously high number of AA activity records were observed (Fig. 1b). During this 5-min period, active AA individuals were registered 44 times (including 22 cases of their simultaneous activity). This behavior was not related to the feeding of animals (as they were not fed either during these 5 min or just before 21:30) and remains unexplained.

In the early phase, the overall level of FF activity (48.8% of activity records observed) was like that of AA (51.2%), so the difference between these values was statistically insignificant (replicated goodness-of-fit tests: $G = 0.058$, $p > 0.05$). In this phase, individuals of both species were most often active at the same time (Fig. 2, category F-A). Such situations occurred significantly more often than the simultaneous activity of only AA shrews ($z = 2.78$, $p = 0.005$) or only FF shrews ($z = 2.81$, $p = 0.005$).

In contrast, in the late phase, AA individuals were more active than FF individuals. For 24 h, 65.1% of the active shrews were AA specimens and only 34.9% were FF. These values differ significantly ($G = 9.264$, $p < 0.005$). It was also noted that two or more AA shrews were simultaneously active significantly more often than two or more FF

individuals ($z = 3.11$, $p = 0.002$) and members of the two species, F-A ($z = 2.57$ $p = 0.010$) (Fig. 2).

Comparison of the simultaneous activity of water shrews between the two phases showed that such activity of FF individuals occurred significantly less frequently during the late phase than the early phase ($z = -2.99$, $p = 0.003$) (Fig. 2). As expected, the frequency of simultaneous activity of the members of two species (F-A) also declined significantly in the late phase ($z = -4.34$, $p < 0.001$). The number of observations of simultaneous AA activity increased slightly in the late phase, but this increase was non-significant ($z = 0.70$, $p = 0.481$) in comparison to the activity of AA in the early phase.

Distances between simultaneously active animals

During the early phase of the experiment, simultaneously active individuals were observed at shorter distances from each other relative to the late phase (Fig. 3). While the differences for the particular groups did not reach statistical significance (FF: $z = 0.54$, $p = 0.587$; AA: $z = 1.43$, $p = 0.154$; F-A: $z = 1.28$, $p = 0.202$), the overall effect of the phase was marginally significant ($\chi^2 = 3.50$, df = 1, $p = 0.061$; Fig. 3).

The average distances between simultaneously active individuals did not differ among particular groups in the
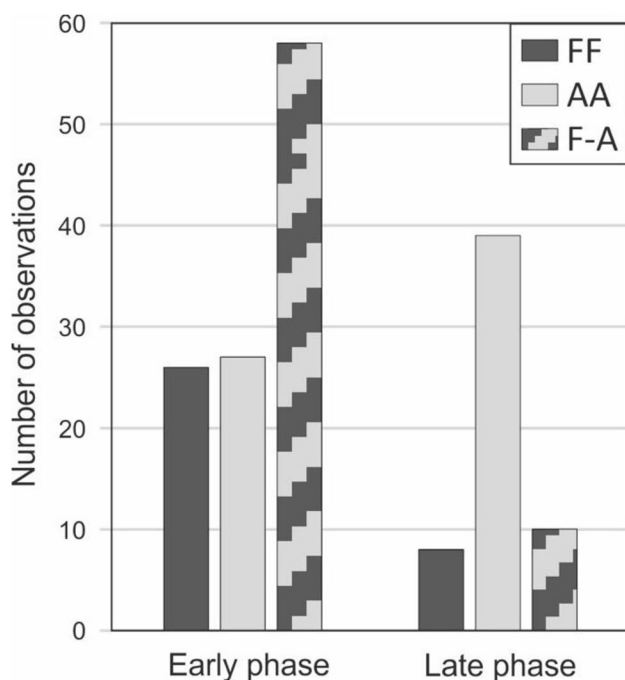

Fig. 2 Simultaneous activity of intra- and interspecific groups of water shrews during the early and late phases of the experiment (FF – two or more *N. fodiens* individuals observed simultaneously outside the nests, AA – two or more *N. anomalus* individuals, F-A – the simultaneous activity of members of the two species)
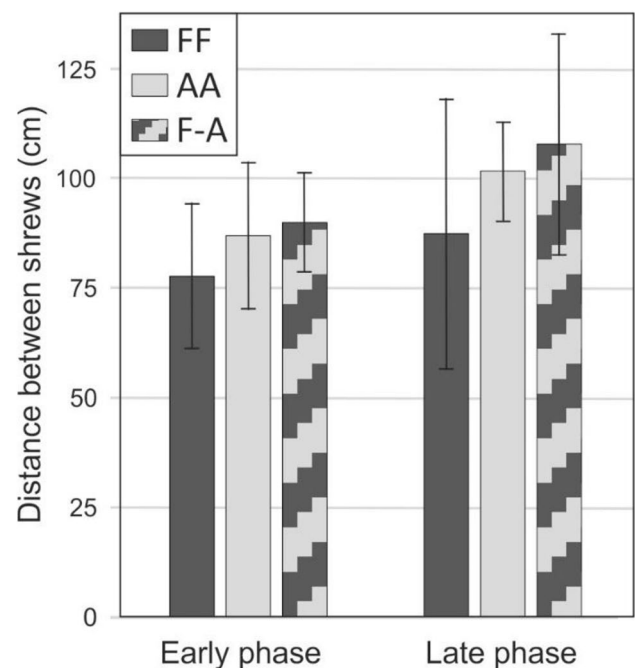

Fig. 3 Estimated average distances maintained between individuals of intra- and interspecific shrew groups simultaneously active during the early and late phases of the experiment (FF—two or more *N. fodiens* individuals observed simultaneously outside the nests, AA—two or more *N. anomalus* individuals, F-A – the simultaneous activity of members of the two species). Whiskers indicate standard errors

early phase (AA vs FF: $z = -0.82$, $p = 0.415$; AA vs. F-A: $z = 0.31$, $p = 0.756$; F-A vs. FF: $z = 1.25$, $p = 0.211$) or the late phase (AA vs FF: $z = -0.86$, $p = 0.392$; AA vs. F-A: $z = 0.46$, $p = 0.644$; F-A vs. FF: $z = 1.05$, $p = 0.294$; Fig. 3) of the experiment. The overall effects of the group and group × phase interaction were non-significant (group: $\chi^2 = 2.55$, df = 2, $p = 0.279$; group × phase: $\chi^2 = 0.14$, df = 2, $p = 0.931$).

However, during the early phase, simultaneously active FF shrews and interspecific groups (F-A) most often kept a medium distance, whereas concurrently active AA individuals were most frequently observed at a short distance from each other (Fig. S2a). During the late phase, simultaneously active interspecific groups (F-A) were most frequently observed in long distances and least often in short distances (Fig. S2b). Surprisingly, a similar tendency was found for simultaneously active AA shrews. In contrast, simultaneously active FF individuals were observed with similar frequency over three distance ranges, which may be related to a more balanced use of the enclosure area and nest boxes by this species.

Usage of nest boxes and feeding trays

We observed the following trends in the usage of nest boxes and feeding trays: (1) AA individuals focused on using only 1–2 nest boxes, while FF individuals were more dispersed in all nest boxes; (2) AA avoided some of the nest boxes occupied by the FF; (3) AA preferred (were most often observed at) feeding trays other than those favored by FF; and (4) the tendency to use different nests and feeders was already displayed by AA and FF in the early phase and remained in the late phase.

Discussion

In the field, the activity of shrews is influenced by natural conditions and their changes: seasons, weather factors, the variety of habitat factors, interactions with other animals, or the activity and availability of prey (Churchfield 1982, 1990; Merritt and Vessey 2000). Under controlled laboratory conditions, most of these factors are usually constant, so interactions with intra- and interspecific competitors may be the main mechanism shaping their circadian activity. For example, it was demonstrated that shrews kept with conspecifics were more active than those kept individually (Goulden and Meester 1978; Barnard et al. 1983). In our enclosure, the mixed group was composed of FF and AA individuals which were concurrently put into the unfamiliar area of the enclosure. During the experiments' first hours, or even days, the animals showed anxiety and increased locomotor activity without a clear rhythm of activity. However,

the animals became accustomed to the new environment and the presence of other shrews over time. Simultaneously, with the stabilization of inter-individual interactions, the number of conflicts decreased (in the late phase of the experiment, no single case of inter- or intraspecific conflicts was recorded). Previous studies also observed a similar pattern (Krushinska and Pucek 1989; Krushinska and Rychlik 1993). These changes may result from both the habituation of one species to the presence of another and some forms of active avoidance of the dominant FF by the submissive AA (Rychlik and Zwolak 2005). These conclusions are also consistent with the results of research conducted on rodents (Ziv et al. 1993).

One such form could be the differentiation of activity rhythms of the two species, which was a change that we observed. During the early phase of the mixed group coexistence, the peaks of FF individuals' activity largely coincided with the peaks of AA activity. In contrast, the activity rhythms of FF and AA became asynchronous in the late phase of the experiment. Representatives of the two species rarely met each other and while the FF individuals were most active, AA individuals were not (Fig. 1b). Therefore, it can be concluded that in 2 months (probably earlier) AA learned to avoid active FF individuals by remaining in the nests, which led to a decrease in the number of conflicts with the dominant competitor. Thus, the H1 hypothesis (that over time, the activity rhythms of AA and FF will differentiate) was supported by our results. In other words, for the first time with shrews, our study demonstrates the competition-induced temporal shift predicted by the theory (Kronfeld-Schor and Dayan 2003; Gao et al. 2020).

During the late phase, it was also noticeable that the peaks in AA activity appeared more frequently and consisted of more activity records than those in FF, so AA tended to be generally more active than FF. These results are consistent with previous findings (Krushinska and Pucek 1989; von Merten et al. 2017), as well as with our H2 hypothesis (AA should display a higher activity level than FF). This can be explained by a higher metabolic rate and greater mass-specific food requirements in AA (Taylor 1998; Rychlik and Jancewicz 2002). Therefore, they also support the general relationship that the circadian activity pattern of a species depends on its metabolic rate — the smaller the species, the higher its metabolic rate, and consequently the higher its activity level.

In the late phase, the simultaneous activity of two or more AA individuals was much more frequent than the simultaneous activity of FF individuals (Fig. 2). This is consistent with the previous observations that AA are more social and tolerant of individuals of their species than FF (Krushinska and Rychlik 1993; Krushinska et al. 1994; Rychlik 1998; von Merten et al. 2017). However, active AA shrews frequently stayed at a short distance from conspecifics only in the early

phase of the experiment. In the late phase, they usually kept a further distance (Figs. 3 and S2). Rychlik and Zwolak (2005) also observed slightly shorter distances between AA individuals in the early phase than late phase of their experiment. This tendency of AA to keep long distances after stabilization of social interaction may be explained in two ways: (1) *N. anomalus* is characterized by very high mobility (Krushinska and Pucek 1989; Rychlik and Zwolak 2005) and (2) although gregarious shrews (as *N. anomalus* but not *N. fodiens*—Krushinska and Rychlik 1993) nest together and are active synchronously, they forage in different places (Rychlik 1998). Such trends have been described for different *Crocidura* species (Shchipanov et al. 1987; Cantoni and Vogel 1989; Shchipanov and Oleinichenko 1993). On the other hand, AA shrews simultaneously active with FF shrews tried to keep some distance from the dominants. This trend intensified in the late phase of the experiment when AA shrews most often stayed at long distances from FF shrews. Thus, the H3 hypothesis was also supported by our results. Keeping a distance from a dominating opponent is one of the effective active forms of conflict avoidance by submissive opponents (Rychlik and Zwolak 2005). Preferences for different nest boxes by AA and FF and mutual avoidance at certain feeding trays also contributed to the reduction of the number of interspecific conflicts.

As mentioned in the 'Introduction', competing species can coexist if they reduce competition by differentiation of certain dimensions of their ecological niches like diet, habitat, or activity time. Under the conditions of our laboratory experiment, the two studied species of water shrews could not diversify their diets or habitats, so they were forced to differentiate the rhythm of circadian activity. Similar mechanisms have been observed before in other small mammals (Kotler et al. 1993; Ziv et al. 1993; Ziv and Smallwood 2000; Adams and Thibault 2006; Castro-Arellano and Lacher 2009) or lizards (Pianka 1973; Kirchhof et al. 2010). We demonstrated that the rhythms of activity of these species became asynchronous in a fairly short time (within 2 months), which was accompanied by a decrease in the number of conflicts and as can be assumed, a diminishing of interspecies interference competition. Since such plasticity of circadian activity has also been observed in rodents (Levy et al. 2007; Cohen et al. 2009) and carnivores (Harrington et al. 2009; Monterroso et al. 2014), we conclude that this is a more common mechanism of reducing interference competition than it has appeared to be in the past.

The additional mechanisms that contributed to this decrease were the maintaining of distances between individuals and the usage limits of the same nests and feeding trays. Moreover, AA (the smaller species with a higher metabolic rate) presented a higher activity level than FF. The frequent simultaneous activity of AA individuals that was observed confirms the greater sociality of this species than of the FF

species. Thus, the results of our experiment seem to support all our hypotheses. Nevertheless, these hypotheses and mechanisms should be tested on larger sample sizes of water shrews, as well as on other competing species.

Declarations

References

Adams RA, Thibault KM (2006) Temporal resource partitioning by bats at water holes. J Zool 270:466–472

Barnard CJ, Brown CAJ, Gray-Wallis J (1983) Time and energy budgets and competition in the common shrew (*Sorex araneus* L.). Behav Ecol Sociobiol 13:13–18

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems, 4th edn. Blackwell Publishing, Oxford

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html. Accessed 10 Nov 2022

Cantoni D, Vogel P (1989) Social organization and mating system of free-ranging, greater white-toothed shrews, *Crocidura russula*. Anim Behav 38:205–214

Castién E, Gosálbez J (1999) Habitat and food preferences in a guild of insectivorous mammals in the Western Pyrenees. Acta Theriol 44:1–13

Castro-Arellano I, Lacher TE Jr (2009) Temporal niche segregation in two rodent assemblages of subtropical Mexico. J Trop Ecol 25:593–603

Churchfield S (1982) The influence of temperature on the activity and food consumption of the common shrew. Acta Theriol 27:295–304

Churchfield S (1990) The natural history of shrews. Christopher Helm, London

Cohen R, Smale L, Kronfeld-Schor N (2009) Plasticity of circadian activity and body temperature rhythms in golden spiny mice. Chronobiol Int 26:430–446

Ferreiro-Arias I, Isla J, Jordano P, Benítez-López A (2021) Fine-scale coexistence between Mediterranean mesocarnivores is mediated by spatial, temporal, and trophic resource partitioning. Ecol Evol 11:15520–15533

Gao VD, Morley-Fletcher S, Maccari S, Vitaterna MH, Turek FW (2020) Resource competition shapes biological rhythms and promotes temporal niche differentiation in a community simulation. Ecol Evol 10:11322–11334

Goulden EA, Meester J (1978) Notes on the behaviour of *Crocidura* and *Myosorex* (Mammalia: Soricidae) in captivity. Mammalia 42:197–207

Halle S (2000) Ecological relevance of daily activity patterns. In: Halle S, Stenseth NC (ed) Activity patterns in small mammals. Ecological Studies, vol. 141 Springer-Verlag, Berlin, Heidelberg, pp 67–90

Hanski I (1985) What does a shrew do in an energy crisis? In: Sibly RM, Smith RH (ed) Behavioural ecology. Ecological consequences of adaptive behaviour. The 25th Symposium of the British Ecological Society, Reading (1984) Blackwell Scientific Publications, Oxford, pp 247–252

Hanski I (1994) Population biological consequences of body size in *Sorex*. In: Merritt JF, Kirkland GL Jr, Rose RK (ed) Advances in the biology of shrews. Special Publication of Carnegie Museum of Natural History No. 18, Pittsburgh, pp 15–26

Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, Macdonald DW (2009) The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression. Ecology 90:1207–1216

Hut RA, Kronfeld-Schor N, van der Vinne V, De la Iglesia H (2012) In search of a temporal niche: environmental factors. In: Kalsbeek A, Merrow M, Roenneberg T, Foster RG (ed) The Neurobiology of Circadian Timing. Progress in Brain Research 199:281–304

Kirchhof S, Linden J, Rödder D, Richter K (2010) Daily activity patterns of *Australolacerta rupicola* (FitzSimons, 1933) (Sauria: Lacertidae) with comments on niche segregation within a syntopic lizard community. North-West J Zool 6:172–181

Kotler BP, Brown JS, Subach A (1993) Mechanisms of species coexistence of optimal foragers – temporal partitioning by two species of sand dune gerbils. Oikos 67:548–556

Krebs ChJ (2009) Ecology: the experimental analysis of distribution and abundance. CA, Pearson Benjamin Cummings, San Francisco

Kronfeld-Schor N, Dayan T (1999) The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. Oecologia 121:123–128

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Annu Rev Ecol Evol Syst 34:153–181

Krushinska NL, Pucek Z (1989) Ethological study of sympatric species of European water shrews. Acta Theriol 34:269–285

Krushinska NL, Rychlik L (1993) Intra- and interspecific antagonistic behaviour in two sympatric species of water shrews: *Neomys fodiens* and *N. anomalus*. J Ethol 11:11–21

Krushinska NL, Rychlik L, Pucek Z (1994) Agonistic interactions between resident and immigrant sympatric water shrews: *Neomys fodiens* and *N. anomalus*. Acta Theriol 39:227–247

Levy O, Dayan T, Kronfeld-Schor N (2007) The relationship between the golden spiny mouse circadian system and its diurnal activity: an experimental field enclosures and laboratory study. Chronobiol Int 24:599–613

Merritt JF, Vessey SH (2000) Shrews – small insectivores with polyphasic patterns. In: Halle S, Stenseth NC (ed) Activity patterns in small mammals. Ecological Studies, vol. 141 Springer-Verlag, Berlin, Heidelberg, pp 235–251

Michalak I (1987) Keeping and breeding the Eurasian water shrew *Neomys fodiens* under laboratory conditions. Int Zoo Yearb 26:223–228

Monterroso P, Alves PC, Ferreras P (2014) Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behav Ecol Sociobiol 68:1403–1417

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Syst 4:53–74

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. Accessed 10 Nov 2022

Rasphone A, Kamler JF, Macdonald DW (2020) Temporal partitioning by felids, dholes and their potential prey in northern Laos. Mammal Res 65:679–689

Roll U, Dayan T, Kronfeld-Schor N (2006) On the role of phylogeny in determining activity patterns of rodents. Evol Ecol 20:479–490

Rychlik L (1998) Evolution of social systems in shrews. In: Wójcik JM, Wolsan M (eds) Evolution of shrews. Mammal Research Institute PAS, Białowieża, pp 347–406

Rychlik L (2004) Competition and coexistence of shrews. In: Jędrzejewska B, Wójcik JM (eds) Essays on Mammals of Białowieża Forest. Mammal Research Institute PAS, Białowieża, pp 161–170

Rychlik L (2005) Overlap of temporal niches among four sympatric species of shrews. Acta Theriol 50. Suppl 2:175–188

Rychlik L, Jancewicz E (2002) Prey size, prey nutrition, and food handling by shrews of different body sizes. Behav Ecol 13:216–223

Rychlik L, Ruczyński I, Borowski Z, Friedrich T (2004) Space use and competitive interactions in shrews (Insectivora: Soricidae) revealed by radio-telemetry. In: Voigt C, Hofer H (ed) Contributions to the 5th international symposium on physiology, behaviour and conservation of wildlife, Berlin, Germany, 26–29 September 2004. Adv Ethol 38, Suppl. to Ethology, p 172

Rychlik L, Zwolak R (2005) Behavioural mechanisms of conflict avoidance among shrews. Acta Theriol 50:289–308

Rychlik L, Zwolak R (2006) Interspecific aggression and behavioural domination among four sympatric species of shrews. Can J Zool 84:434–448

Saarikko J, Hanski I (1990) Timing of rest and sleep in foraging shrews. Anim Behav 40:861–869

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39

Shchipanov NA, Oleinichenko VYu (1993) [The bicoloured white-toothed shrew. The behaviour and spatial, ethological, and functional structure of a population]. Nauka, Moscow [In Russian]

Shchipanov NA, Shilov AI, Bodyak ND (1987) Behaviour of *Crocidura suaveolens* observed in confinement. Zool Zurnal 66:1540–1552 ([In Russian])

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. WH Freeman, New York

Taylor JRE (1998) Evolution of energetic strategies in shrews. In: Wójcik JM, Wolsan M (eds) Evolution of shrews. Mammal Research Institute PAS, Białowieża, pp 309–346

Tsunoda H, Newman C, Peeva S, Raichev E, Buesching CD, Kaneko Y (2020) Spatio-temporal partitioning facilitates mesocarnivore sympatry in the Stara Planina Mountains, Bulgaria. Zoology 141:125801. https://doi.org/10.1016/j.zool.2020.125801

Vernes K, Rajaratnam R, Dorji S (2022) Patterns of species co-occurrence in a diverse Eastern Himalayan montane carnivore community. Mammal Res 67:139–149

Vogel P (1976) Energy consumption of European and African shrews. Acta Theriol 21:195–206

von Merten S, Zwolak R, Rychlik L (2017) Social personality: a more social shrew species exhibits stronger differences in personality types. Anim Behav 127:125–134

Ziv Y, Abramsky Z, Kotler BP, Subach A (1993) Interference competition and temporal and habitat partitioning in two gerbil species. Oikos 66(2):237. https://doi.org/10.2307/3544810

Ziv Y, Smallwood JA (2000) Gerbils and heteromyids – interspecific competition and the spatio-temporal niche. In: Halle S and Stenseth NC (ed) Activity patterns in small mammals. Ecological Studies, vol. 141 Springer-Verlag, Berlin, Heidelberg 159–176

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