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Research Article

Behavioural and population responses of ground-dwelling rodents to forest edges

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Abstract

Forest edges can affect the behaviour, physiology and demography of small mammals. We tested whether there was a response in abundance, distribution, personality selection or foraging behaviour of ground-dwelling rodents to a forest–meadow edge in two study areas in Northern Italy over a 1-year period. We used capture-mark-recapture to evaluate species distribution, abundance, survival and personality, while Giving-up Density was used to test their foraging behaviour and the cost associated to it. All tests were carried out on the forest edge and at 50 and 100 m from the edge along three parallel transects 90 m long. We detected two species in both areas: *Apodemus sylvaticus* and *Myodes glareolus*. We found a neutral effect of the edge on species number, survival and on individual's personality (activity/exploration tendency). Bank voles occurred more along the edge and both taxa took more seeds from trays along the edge. The hypothesis of edge avoidance was not confirmed in any of the variables examined. Our study supports evidence that edge effects can be species-specific and that populations should be studied with a multiple test approach to investigate different eco-ethological responses to the edge when trying to reveal the functioning of ecotonal systems.

Introduction

Human-alteration of forested landscapes has increased both the destruction of suitable forest habitat for many species and the proportion of forest area that lies close to an edge. The forest edge becomes part of a transition zone or ecotone, that usually exhibits differences in microclimate, species composition and vegetation structure compared to forest interior (Murcia, 1995; Saunders et al., 1991; Schnurr et al., 2004). Hence, a habitat edge can be considered a spatial discontinuity that affects in some way an animal species' behavioural, physiological or demographic performance (Lidicker and Peterson, 1999).

Forest edges can affect mammals in their abundance, distribution and occurrence (Kremsater and Bunnell, 1999; Murcia, 1995; Nams, 2012). The magnitude of these effects depends both on the quality of the habitat on both sides of the edge and the extent of human activity at the edge of the forest, as well as the species under consideration. Rodents, because of their restricted vagility, may be more susceptible to the edge effect, particularly for species that are not habitat generalists (Schmid-Holmes and Drickamer, 2001). Small mammals' distribution in temperate forests is influenced by 3 main factors: resource availability, as food, water or nest sites (Barnum et al., 1992; Bisi et al., 2016; Getz, 1968); predator avoidance (Morris and Davidson, 2000; Orrock et al., 2004; Thorson et al., 1998); competition with other species (Jones et al., 2001; Mazzamuto et al., 2017; Yunger et al., 2002). These factors can be altered by the habitat edge; for example, a higher mortality of small rodents through increased predation related to a higher occurrence of predators along the edge, and/or a lower plant cover that protects the prey (Ferguson, 2004; Morris and Davidson, 2000; Orrock et al., 2004). Small mammals play an important role in the regulation of many processes supporting natural ecosystems. They are not just an abundant and widespread prey indispensable for numerous other vertebrates (Bontzorlos et al., 2005; Lozano et al., 2006; McDonald et al., 2000), but they are also primary consumers that can actively contribute to the regeneration and expansion of numerous habitats through secondary seed-dispersal (Chang and Zhang, 2011; Schnurr et al., 2004; Vander Wall, 1990; Wauters and Casale, 1996). With a worldwide increase in amount of edge habitat as consequence of forest fragmentation, studying how small mammals respond to these changes will increase our understanding of the functioning of fragmented habitats (Donoso et al., 2004; Pfeifer et al., 2017).

In this study we test the abundance, survival, distribution and foraging behaviour of ground-dwelling rodents along the forest edge. Moreover, we also want to test a possible selection in personality traits along the edge using indirect indices of personality. Among small mammals, an individual's willingness to enter a baited trap can be considered an indication of its propensity for risk-taking, because it accepts the risks associated with trapping and handling in order to obtain a food reward (Réale et al., 2000). So individual trappability is often used as a measure of boldness, while the number of different traps visited by an individual is used as a measure of explorative behaviour (Bohn et al., 2017; Boyer et al., 2010; but see Brehm and Mortelliti, 2018).

Previous studies reported neutral effects of habitat edges on small mammal's populations (e.g. Anderson et al., 2006), positive effects (edge attraction; e.g. Lidicker and Peterson, 1999; López-Barrera et al., 2005) or negative effects (edge avoidance; e.g. Delattre et al., 2009; Stevens and Husband, 1998). We hypothesize the case of edge avoidance, with the edge characterized by a lower number of species and/or abundance, a lower survival along the edge and a lower food harvest rate. Moreover, we expect relatively bolder animals living on the edge than inside the forest, since individuals with risk-taking personality trait are more likely to face the increased predation risk than shy individuals.

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Materials and methods

Study areas and design

Ground-dwelling rodents were studied from June 2016 to April 2017 in two areas of Pineta di Appiano Gentile and Tradate Regional Park (Lombardy, Italy), an area of 4828 ha characterized by acidophilic forests of broadleaf and conifers, and mesophilic forests. Forests cover about 3000 ha, while agricultural land is composed of stable meadows (275 ha) and crops (1325 ha). At each of the two study areas (A and B) we established 3 transects 90 meters long that ran parallel along a forest–meadow edge and reached 100 m into the interior of the forest. The first transect was at the edge while the second and third were at 50 m and 100 m, respectively, with their sides at least 50 m and 100 m from any other forest edge. Area A had the edge 200 m long with a meadow of 2 ha in front while at area B the edge was 215 m long with 3 ha of meadow. The two areas were 1500 m far apart. A detailed vegetation study of both areas is reported in Supplementary material S1.

Trapping and handling

In both areas, along each of the three transects, 10 single large Sherman traps (7.5×9×23 cm; HB Sherman Traps Inc. Tallahassee, Florida, USA) were spaced 10 m for a total of 30 traps/area. Trapping was conducted in 6 trap periods at each area during June, July, September, October (2016), March and April (2017). During each trap period, traps were active for three consecutive nights and checked early in the morning and before sunset for a total of 6 controls per trap period (trap rounds). Live traps were baited with a mixture of sunflower seeds, Nutella, a piece of potato to avoid dehydration, and a handful of hydrophobic cotton was added so that the captured rodents could make a nest to keep warm until they were marked and released. Captured individuals were identified to species level and subsequently sexed, aged, weighed and permanently marked with passive integrated transponder tags (RealTrace 2016; size=1.4×8.5 mm). Animals were released at the place of capture. All the procedures of trapping and manipulation of animals took place in compliance with the European Council Directive 92/43 EEC (Italian law D.Lgs 157/92 and LR 3/1994) and with the Directive 2010/63/EU (Italian law D.Lgs 116/92).

Foraging experiment

We examined differences in the foraging behaviour of ground-dwelling rodents between the three transects in each study area. We used two aluminium trays per transect (2 l capacity each; 6 trays per area) filled with 2 l of sand mixed with 30 g of black oil sunflower seeds. The seed trays were set out on the field 24 h every month from June 2016 to April 2017 and every month they were semi-randomly placed along each transect to occupy the majority of the sites along it. The pair of seed trays per transect was spaced at least 30 m apart. During the 24 h, a first control consisted of sifting the sand and collecting all remaining intact seeds after 12 h followed by refilling the tray with sand and mixing it again with other 30 g of sunflower seeds. The second and final control after another 12 h, consisted of sifting the sand and collecting the remaining full seeds. Each time the sifted seeds were air-dried and the mass was measured to determine the Giving-up Density (GUD), that indicates when the benefit obtained from foraging is balanced by the summed energetic costs, the risk of predation, and the missed opportunity cost of not engaging in alternative activities (Brown, 1988).

The experiment was carried out when the areas were not involved in trapping activities.

Data analysis

Our data were analysed to test for an effect of the forest edge on population parameters, personality and foraging behaviour. The transect where data were collected was used as a factor to represent the distance from the edge (transect 1=on the edge; transect 2=50 m; transect 3=100 m). Moreover, our data were collected in two different areas that account for pseudoreplicates, hence the factor "area" was always included in our models as a random factor to take into account possible differences between study areas. Since the edge effect can be species specific (Lidicker, 1999), all analyses were carried out separately for each species.

Population parameters

Because of species low capture-recapture rates in this study, population size (N) was estimated using the minimum number of animals known to be alive (MNA, Krebs, 1999) from trapping data of each trap period. A Poisson regression was used to test for differences in N: we considered the transect (hence distance from the edge) as explanatory variable in a Generalised Linear Mixed Model (GLMM, R package `lme4` v 1.1-12) with season (March– May=spring; June–August=summer; September–November=autumn) added as a factor to control for seasonal fluctuations in rodent numbers. Study area was added as random factor to account for pseudoreplications and trap period nested in season as a second random factor to account for repetitions in time. Differences in least square means (DLSM) with the Tukey *p*-value adjustment for multiple tests were used to identify significance in pairwise comparisons.

The catch per unit effort (cpue) of each species per area over the entire study period (number of individuals trapped/number of occasions) was calculated, and the number of trapping events for each species per area over the entire study period was compared using a χ^2 test.

Local survival for each species was estimated using Kaplan-Meier survival curves (Kaplan and Meier, 1958). Proportional Hazard Regression (Cox, 1972) was used to test for differences in survival between transects and sexes with data stratified per area.

Indirect indices of personality

To assess individual consistency for trappability we estimated the repeatability (Bell et al., 2009), also called Intra-class Correlation Coefficient (ICC), of the number of capture events (n_capt) of each individual at each trap period with Linear Mixed Models (LMM, `lme4` package; Bates et al., 2014). "n_capt" was the dependent variable, "ID" the random intercept term, to estimate the % variance explained by repeated measures on the same individual, and sex and trap period were included as fixed effects. Repeatability was estimated using the R package `rptR` v 0.9.2 (CI=95%, number of parametric bootstraps for interval estimation=5000, number of permutations used when calculating asymptotic *p*-values=1000) (Bohn et al., 2017; Stoffel et al., 2017). Following Martin et al. (2011), we included individuals with one measurement in our repeatability analysis to increase power. Next we explored whether animals living on the edge were more bold than forest interior animals (transect effect). We used Generalised Linear Mixed Models (GLMMs, Bolker et al., 2009) with "n_capt" as dependent variable, "transect" and "sex" as fixed effects, using the ID and area as random effects.

The same process was followed for the estimate of the repeatability of trap diversity using the number of different traps were an individual was captured at each trap period as dependent variable and for the following GLMM. Statistical analyses were carried out separately for each species using the R package `lme4` ver. 1.1-12 for fitting and analysing mixed models (Bates et al., 2014).

Foraging experiment

A GLMM (R package `lme4` ver. 1.1-12) was used to test for differences in GUD between transects. Factor "season" was added as a factor to account for potential effects of seasonal fluctuations on the GUD, while "area" as a random factor to account for pseudoreplicates. Differences in least square means (DLSM) with the Tukey *p*-value adjustment for multiple tests were used to identify significance in pairwise comparisons.

Results

Population parameters

A total of 36 trap rounds (6 per trap period) of 30 different traps were carried out from June 2016 to April 2017 in each of the 2 areas. *Myodes glareolus* and *Apodemus sylvaticus* were the only two granivorous rodents trapped in all transects. Only four other non target individuals

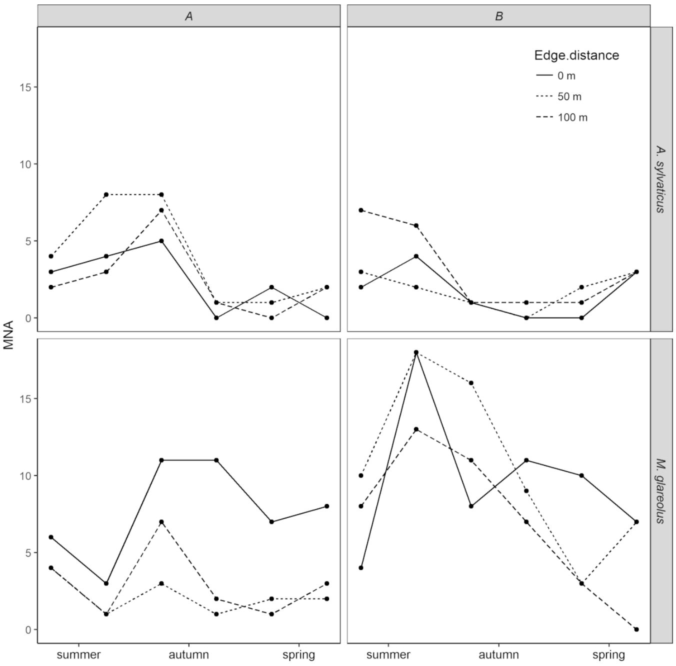

Figure 1 – Average Minimum Number of animals known to be Alive (MNA) per season for the species *Apodemus sylvaticus* and *Myodes glareolus* in each study area and at different distances from the edge.

were trapped (*Crocidura leucodon*, *Sorex* sp.). In area A 47 different bank voles were captured (22 males, 25 females, total captures 148, cpue 4.11) against 107 in area B (42 males, 65 females, total captures 327, cpue 9.08). Forty-five different wood mice were trapped in area A (26 males, 19 females, total captures 86, cpue 2.39) and 34 in area B (21 males, 13 females, total captures 74, cpue 2.06). The catch per unit effort in both areas was significantly higher for bank vole than for wood mouse (χ^2 test=25.3, df=1, p<0.001).

There was no difference in the abundance of wood mice between the edge and the forest interior (all p>0.05) or between seasons (all p>0.05) (Fig. 1; Tab. S2, S3). In contrast, bank vole numbers were affected both by the distance from the edge and by season. In the interior of the forest vole numbers were lower than at the edge (transect 2−transect 1: -0.31 ± 0.15, z=-2.08 p=0.04; transect 3−transect 1: -0.55 ± 0.16, z=-3.40 p=0.0007) and there were fewer voles in spring than in summer and autumn (spring−summer: -0.53 ± 0.19, z=-2.75 p=0.02; spring−autumn: -0.60 ± 0.19, z=-3.17 p=0.004) (Fig. 1). Overall, 9 voles and 6 mice in their trapping history were caught in 2 adjacent transects (different trapping periods), but since in our analyses the sample unit was the trapping period, this didn't affect our results.

Kaplan-Meier survival rate for bank voles was 0.31 after 1 month (95% CI 0.25–0.40) and 0.04 (95% CI 0.02–0.09) after 7 months, while for the wood mouse it was 0.14 (95% CI 0.08–0.25) after 1 month and 0.007 (95% CI 0.0006–0.09) after 7 months. Local survival for both species did not differ between sexes or transects (bank vole: Likelihood ratio test=1.2, df=3, p=0.75; wood mouse: Likelihood ratio test=4.74, df=3, p=0.19).

Indirect indices of personality

On average (±SD), wood mice were captured 1.62 ± 0.85 times/trap period and trapped in 1.40 ± 0.59 different traps. Bank voles were captured on average 2.11 ± 1.42 times/trap period and trapped in 1.50 ± 0.75 different traps. Trappability and trap diversity indices were not significantly consistent within individuals of *A. sylvaticus* (both p>0.05) but were repeatable for *M. glareolus* (trappability R=30%, 95% CI=12–52%, LRT=12.3, df=1; p=0.0002; trap diversity R=30%, 95% CI=12–51%, LRT=15.1, df=1; p<0.0001). Hence, personality could only be analysed for bank voles.

Trappability and trap diversity of bank voles did not differ with distance from the edge or with sex, hence bold animals and/or animals with a strong tendency to explore were homogeneously distributed without a preference for edge or interior habitats (Tab. 1).

Table 1 – Comparison of indirect indices of personality of *Myodes glareolus* at different distances from the forest edge (transect) and between sexes (M: males, F: females; see methods for details).

	Contrast	**Estimate ± SE**	**z**	***p***
Trappability	transect 1−2	0.17 ± 0.11	1.51	0.13
	transect 1−3	0.22 ± 0.12	1.82	0.07
	M−F	0.05 ± 0.10	0.52	0.6
Trap diversity	transect 1−2	0.24 ± 0.13	1.76	0.08
	transect 1−3	0.21 ± 0.14	1.55	0.12
	M−F	0.06 ± 0.11	0.54	0.59

Foraging experiment

Using camera traps set in video-mode in front of the trays allowed us to verify that only bank voles and wood mice pilfered seeds from the trays. The Giving-up Density was lower on the edge than the interior of the forest (transect 1−transect 2: -3.77 ± 0.10, df=232, t=-3.42 p=0.0007; transect 1−transect 3: -3.33 ± 0.10, df=232, t=-3.02 p=0.003) and on average it was lower in summer than in all other seasons (DLSM all p<0.0001) (Tab. 2, S4).

Discussion

We explored effects of forest–meadow edges on ground-dwelling rodents' populations in Northern Italy. All our tests were conducted at different distances from the edge to detect possible responses to the edge. We detected a neutral effect of the edge on the number of species present, survival and on individual's personality, a species-specific edge-effect on abundance, and a positive effect (edge attraction) on foraging behaviour. The hypothesis of edge avoidance was not confirmed in any of the variables examined. The limitations of this study in terms of time period and sample size, in particular for small mammals that are affected at a small scale by different environmental and ecological factors, prevent us from making broader generalizations from our results, but we think that this study is a good example of a multiple approach to a wide ecological topic as "edge effect".

We did not find any difference in species number between the edge and the interior of the forest. We trapped in both areas the bank vole *M. glareolus* and the wood mouse *A. sylvaticus*. The wood mouse lives both in open (grasslands and fields) and forested areas and has generalist food habits (Gasperini et al., 2018; Sozio and Mortelliti, 2016; Sunyer et al., 2016). The distribution we recorded is in agreement with the generalist behaviour and the predominantly nocturnal activity of wood mice (Eldridge, 1968; Sunyer et al., 2016). In contrast, bank voles can be found in a variety of habitats but they are mainly associated to forest habitats with a good ground cover and shrub structure, that increase protection from bird and mammal predators (Gasperini

Table 2 – Giving-up Density for each area, transect and season. Trays were filled with 2 l of sand and 30 g of sunflower seeds and checked every 12 hours (see methods for details).

		area A		**area B**	
		mean (g)	**± SD**	**mean (g)**	**± SD**
Transect	1	24.57	6.42	19.96	8.72
	2	25.84	8.54	25.91	7.76
	3	26.54	6.45	24.9	8.44
Season	summer	21.55	4.05	14.85	11.71
	autumn	26.56	6.26	24.3	7.26
	winter	27.22	5.89	26.57	5.46
	spring	27.53	4.05	26.79	4.4

et al., 2016; Macdonald, 2001; Mazurkiewicz, 1994). Even though in our areas shrub cover was higher along the edge, bank voles used both the edge and the forest interior. However, voles were more abundant at the edge than at the forest interior. Since vole survival was not affected by the distance from the edge, the lower number of individuals in the interior of the forest may be related to the preference for high cover habitat. Studies on other species of small mammals reported contrasting results about the effect of forest edges on population abundance, with less (Delattre et al., 2009; Stevens and Husband, 1998) or the same number of individuals (Anderson et al., 2003; Tallmon and Mills, 2004) along the edge than inside the forest, sometimes finding different results for the same species (e.g. *Peromyscus leucopus*; Anderson et al., 2006; Wolf and Batzli, 2002). Mills (1995) suggested that differences between the edge and the forest interior may be related more to the different forest productivity than the habitat structure itself. In our study areas, further investigations on forest productivity should be carried out to confirm if the distribution of bank voles is related more to the habitat structure (understorey cover) or to food availability (Manson and Stiles, 1998; Wolf and Batzli, 2004).

Forest edges are often associated to higher mortality of small rodents because of increased predation risk related to a higher occurrence of predators along the edge, and/or a lower plant cover that protects the prey (Ferguson, 2004; Morris and Davidson, 2000; Orrock et al., 2004). In this study we did not find a difference in survival between the edge and the interior of the forest, nor did we find differences between sexes. The predators of ground-dwelling rodents in Pineta di Appiano Gentile e Tradate Regional Park are many species of birds of prey and owls (e.g., kestrel, common buzzard, tawny owl, long-eared owl), some snakes (e.g., green whip snake, Aesculapian snake) and carnivores as badger, red fox and beech marten. Our result suggests that predation pressure in the area is uniform and that the edge does not increase the mortality of voles and mice. Previous studies showed that rodents' activity and occurrence is related to indirect (microhabitat) and not direct (olfactory and visual) cues of predation risk (Orrock et al., 2004; Sivy et al., 2011; Thorson et al., 1998). Thus the presence of small mammals is more related to factors such as ground cover, refuges, visibility to reduce the risk of predation than to the actual presence/activity of predators. This may also be the reason why we did not find any selective use of edges by ground-dwelling rodents with certain personality traits: in our study areas bold voles and/or animals with a strong tendency to explore were homogeneously distributed without a preference for edge or interior habitats. Unfortunately, the two indirect personality indices used were not reliable for the wood mouse, probably because of a low capture-recapture rate of the species resulting in lack of repeatability of these indices (see Brehm and Mortelliti, 2018). In the future further analyses using direct measures of personality (e.g. open field test) and the correlation between personality traits and trappability would clarify the issue (Brehm and Mortelliti, 2018; Carter et al., 2013).

Processes such as plant-plant interactions, plant-animal interactions and forest regeneration can be altered in their dynamics by the habitat bordering the forest and the forest edge itself (e.g. Donoso et al., 2004). We tested the effect of the edge on the foraging behaviour of mice and voles in our areas. Wood mice and bank voles are known to be seed consumers (Gasperini et al., 2018) but they also cache food to enhance survival in periods of low food availability (like the winter time) and to improve reproductive success during the breeding period (Hansson and Henttonen, 1985; Mappes, 1998; Sunyer, 2015; Vander Wall, 1990). Based Giving-up Denstiy (GUD) theory, a high GUD suggests a low benefit from foraging in a given patch compared to the summed costs of energy consumption, predation risk and missed opportunities of not engaging in alternative activities (Brown, 1988; Olsson and Molokwu, 2007, but see Price and Correll, 2001). Our results showed a lower GUD, thus a greater seed predation, from trays along the edge than inside the forest, indicating high benefits of feeding along the edge. Some studies reported similar results (Kollmann and Buschor, 2003; López-Barrera et al., 2005) while others reported higher foraging activity inside the forest (Moenting and Morris, 2006; Morris and Davidson, 2000; Vaaland Burkey, 1993). We argue that lower GUD along the edge in our study was associated to differences in microhabitat (ecotonal effect, see Lidicker, 1999). Our vegetation study showed that ground cover along the edge was higher than inside the forest, suggesting a higher benefit of foraging at the edge because of lower predation risk linked to better cover (Birney et al., 1976; Bowers et al., 1993; Brown et al., 1992; Thorson et al., 1998)). López-Barrera et al. (2005) suggested that the edge can act as a barrier and animals may spend more time travelling along the edge and incidentally could encounter food resources, but since our measure of trap diversity (number of different traps in which an individual was caught) was the same at the edge and in the forest, we exclude this hypothesis.

We found seasonal differences in the abundance of bank voles and in GUD. There were fewer bank voles in spring than in summer and autumn. This trend may be related to a reduction of the population size during the winter (when no trapping occurred) because of a high mortality due to low temperatures and lack of food resources (Crawley, 1970; Olsson et al., 2002; van Apeldoorn et al., 1992)). Moreover, the GUD was lower in summer than in all other seasons; hence voles and mice spent more time feeding on the trays in summer. During this season the understorey of the forest and ground cover is generally denser probably reducing the predation risk perceived by ground-dwelling rodents. Temporal variation in the availability of food resources in the forest can also play a role in seasonal changes of the GUD (Brown et al., 1992; Olsson et al., 2002). If this was the case in our study, we would expect a stronger attraction of artificial food, and thus a lower GUD, mainly during the winter–early spring, which was not recorded.

Conclusions

In our study we predicted a negative (edge avoidance) response of ground-dwelling rodents to ecotonal habitat. The analyses found positive or neutral responses to the edge (even within the same species) depending on the parameter measured (e.g., number of species and distribution, foraging behaviour). Many studies have tried before to extract general conclusions on the presence or not of an edge effect on animal populations. Our study, despite its limitations in terms of sampling effort, suggests that responses to edge effects should always be considered species specific (in some cases even sex and age specific; see Lidicker, 1999) and that patterns should be investigated with a multiple test approach to explore different eco-ethological responses to the edge.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplementary material S1 Vegetation study.

Table S2 Generalized Linear Mixed Model (GLMM) testing for the effects of transect and season on wood mice abundance.

Table S3 Post-hoc test using Differences in Last Square Means (Tukey *p*-value adjustment) on the GLMM.

Table S4 Post-hoc test using Differences in Last Square Means (Tukey *p*-value adjustment) on the GLMM.