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SIZE OF THE VOMERONASAL ORGAN IN WILD *MICROTUS* WITH DIFFERENT MATING STRATEGIES*

LISETTE M. MAICO,[1,2]** ANNIE M. BURROWS,[3,4] M. P. MOONEY,[3,5] M. I. SIEGEL,[3] K. P. BHATNAGAR,[6,7] and T. D. SMITH[2,3,7]

[1] Rehab Department, Southland, Norwalk, CA 90650, USA
[2] School of Physical Therapy, Slippery Rock University, Slippery Rock, PA 16057, USA
[3] Department of Anthropology, University of Pittsburgh, Pittsburgh, PA 15260, USA
[4] Department of Physical Therapy, Duquesne University, Pittsburgh, PA 15282, USA
[5] Department of Oral Medicine and Pathology, University of Pittsburgh, Pittsburgh, PA 15260, USA
[6] Department of Anatomical Sciences and Neurobiology, University of Louisville, School of Medicine, Louisville, KY 40292, USA
[7] Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, PA 15206, USA (affiliated)

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Most studies on mammalian vomeronasal organ (VNO) have been on laboratory-bred animals. Our present study examines the VNO in wild-caught meadow voles (*Microtus pennsylvanicus;* n = 16) and prairie voles (*M. ochrogaster;* n = 15). These species vary in their mating strategies and degree of parental care by males. *M. ochrogaster* exhibits pair bonding and more paternal care compared to *M. pennsylvanicus,* a promiscuous species. We hypothesize that sexual dimorphism will occur in the promiscuous species based on previous studies which suggest that those who exhibit more aggressive or masculine behavior have larger VNOs. Our results support our original finding that VNOs are not different in size in wild *Microtus spp.* that vary in male parental tendencies. However, the present study also indicates that *M. pennsylvanicus,* the species exhibiting more disparate parental tendencies, exhibited larger VNOs in females than males. This is the reverse of previous findings on rats, and we hypothesize that this difference may be due to mate selectivity and/or maternal aggression.

Keywords: Mate selectivity – vomeronasal neuroepithelium – chemosensory

INTRODUCTION

The mammalian vomeronasal organ (VNO) is a paired, chemosensory epithelial structure located within the base of the nasal septum. Each VNO structure is composed of the vomeronasal neuroepithelium (VNNE) and the receptor-free epithelium (RFE). Functionally, the vomeronasal system has been linked to various behaviors such as mate-finding and the level of parental tendencies [11, 14, 24]. Factors related to VNO size are not well understood, but some researchers have suggested links to endocrine factors [13, 14]. More recent studies have shown that this relationship is not clear in all mammals [17, 21].

* A preliminary report of this work was presented at the *Chemical Signals in Vertebrates 9* (see [7])

** Corresponding author; e-mail: lismaico@hotmail.com

Many studies on the VNO have focused on laboratory-bred animals [13, 21, 22]. Segovia and Guillamón [14] suggest that their laboratory-bred rats exhibited a positive correlation between larger accessory olfactory structures and decreased level of parental care by males. According to them, rats with larger VNOs (males) have an increased tendency to exhibit more "masculine" behavior (e.g., aggressive, less paternal). Furthermore, Shapiro et al. [15] found that regions of the brain that receive input from vomeronasal system are sexually dimorphic in voles with different mating strategies.

Our own study focuses on two species of wild-caught voles: *M. ochrogaster* and *M. pennsylvanicus*. Pair-bonding is seen in *M. ochrogaster*, where the males are more active participants in parental care than the males of *M. pennsylvanicus* [3, 10]. Thus, if we agree with the hypothesis that a larger VNO correlates with a more aggressive/masculine behavior, *M. pennsylvanicus* should exhibit greater sexual dimorphism (male > female) in VNO size compared to *M. ochrogaster*. A preliminary study by our group [7] on the same species of *Microtus* did not precisely support this hypothesis. Instead, our findings indicated proportionately larger VNO volumes in female *M. pennsylvanicus*, in contrast to the findings of Segovia and Guillamón [13]. Furthermore, a study by Smith et al. [17] on the size of the VNNE in wild *M. pennsylvanicus* and *M. ochrogaster* did not support the hypothesis that VNNE size is negatively associated with the level of parental care by male voles. In both studies, VNO size was quantified by the overall length and volume of the VNNE. The purpose of this study is to further quantify the VNNE via receptor cell counts and cross-sectional area at multiple rostrocaudal positions. Using VNO volume, length, and estimates of receptor cell populations, the present study tests the hypothesis that *M. pennsylvanicus* shows greater sexual dimorphism (due to more disparate parental tendencies) than *M. ochrogaster*.

MATERIALS AND METHODS

Collection of animals

For our study, *M. pennsylvanicus* (8 males, 8 females) and *M. ochrogaster* (8 males, 7 females) were captured between June and August 1998. Specimens were live-trapped in Pittsburgh or Slippery Rock, Pennsylvania (*M. pennsylvanicus*) and Bloomington, Indiana or Effingham, Illinois (*M. ochrogaster*). Each animal that was suitable (based on adult size) was euthanized by cervical dislocation and immediately immersed in 10% buffered formalin (Fisher Scientific, Pittsburgh, PA). It was subsequently found that all males had histologically identifiable evidence for spermatogenesis, including the presence of late spermatids [7]. All females exhibited corpora lutea in the ovaries or were pregnant (5 of 8 *M. pennsylvanicus* and 3 of 7 *M. ochrogaster* were pregnant at the time of capture). Prior to histology, palatal length was measured. Heads and gonadal tissues were processed at the Basic Science Research Laboratory in the Graduate School of Physical Therapy, Slippery Rock University.

Tissues were embedded in paraffin and sectioned at 16 μm (5 specimens) or 10 μm (all others). Every tenth section was mounted on numbered glass slides, stained with hemotoxylin-eosin, and examined under light microscope. Selected sections were stained with Gomori trichrome procedure. More detailed explanations of how the voles were trapped, selected, and prepared for histological assessment are provided in Smith et al. [17].

Statistical analysis

Measurements of each specimen were taken at the University of Pittsburgh in the Image Processing Laboratory, Department of Anthropology and in the Neurohistology Laboratory at Slippery Rock University. For all measurements, we arbitrarily used the right VNO since an earlier study indicated that there were no significant differences between right and left sides [17]. Vomeronasal neuroepithelial length (VNNEL) was calculated by summing up the recorded thickness of all the sections in which the VNNE was found. Volume quantification was done using three-dimensional reconstruction technique [16]. Ratios of VNNE lengths and volumes (VNNEV) to palatal lengths were calculated to control for any differences that may result solely from body size differences. These ratios were converted using the arcsine transformation prior to statistical analysis [18].

The first rostrocaudal section in which VNNE was found was designated as being "zero percent" and the last section was designated as "100 percent". Based on these start and stop points, we calculated sectional levels for the 25th percent, 50th percent, and 75th percentiles. Every attempt was made to use the exact section of the VNNE for collecting data. However, in cases where these sections were damaged or difficult to photograph, the previous or next section was used. At each percentile, the VNO was magnified (×600) and digitally photographed using Pixera Visual Communications Suite 2.0 software. Photographs were taken from three parts of the VNNE (dorsal, middle, and ventral) and were used for an average count at each percentile. Therefore, three values are recorded for each percentile (25th, 50th, and 75th percentile), making a total of nine recordings for each specimen. After digitally photographing a stage micrometer, a 40×40 μm grid was constructed using Adobe Photoshop 4.0. This grid was, then, superimposed over the three regions of VNNE (dorsal, middle, ventral) using Adobe Photoshop 4.0. Care was taken not to position the grid in the proliferative zones of VNNE near the dorsal and ventral intersections with the receptor-free epithelium (Fig. 1). Receptor cell nuclei are located in the middle stratum of the vomeronasal epithelium with nuclei that appear rounder than more apical supporting cells; basal cells are triangular and lie close to the basement membrane. Care was also taken to position the grid in such a way as to exclude supporting cell or basal cell nuclei. A receptor cell was included if at least half of its nucleus fell within the borders of the grid. Using the Adobe Photoshop paintbrush tool, nuclei were marked during the counting to avoid counting cells more than once. Variation in the thickness of sections may have an effect on the number (and densi-

ty) of nuclei appearing in cross-section. To avoid this, only 10 µm sections were analyzed in cell counts. Since cell count comparisons are only being made within this sample, and only using specimens that were prepared similarly, a correction factor was not needed [see also 1].

Average cell counts (of dorsal, middle, and ventral VNNE) were calculated for the 25th, 50th or 75th percentiles. The number of receptor cells per 40 × 40 µm grid was then converted to the number per mm^2 for tabulation (Table 2). In order to provide further information on the distribution of receptor cells throughout the VNO, area of the VNNE (obtained automatically via the digitizing method described in [16, 17]) was recorded at the same percentiles. Prior to statistical analysis, plots were generated using SPSS 11.0 software and were examined for possible outlying data points. Dixon's test [18] was used to determine whether these should be removed.

Length and volume data were analyzed using a 2-way (species × sex) Analysis of Variance (ANOVA). Since some of the data were not normally distributed, transfor-

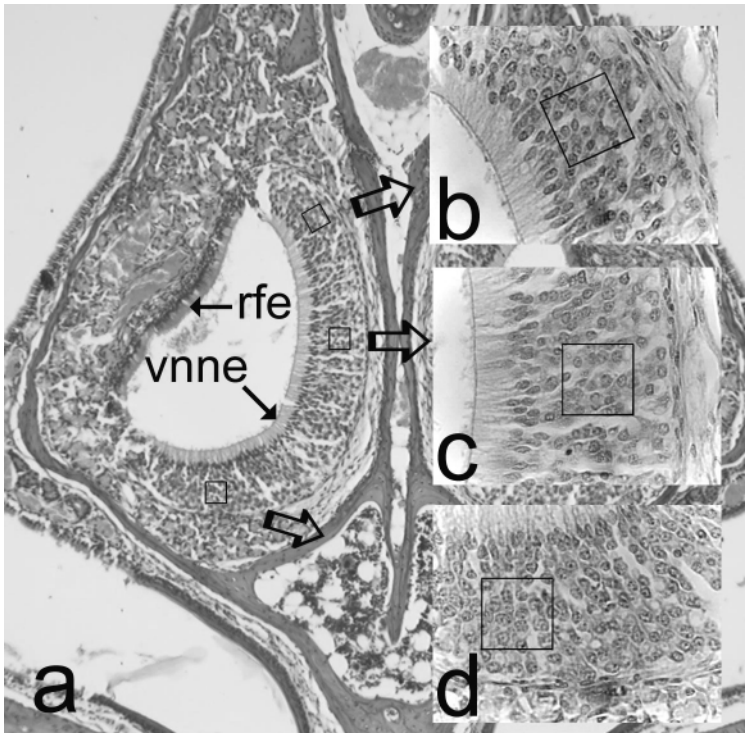


Fig. 1. (a) Coronal section of the right VNO in *Microtus pennsylvanicus* showing the thinner, lateral receptor-free epithelium (rfe) and thicker, ventromedial neuroepithelium (VNNE). The open arrows show the region for the cell counts in the dorsal (b), middle (c), and ventral (d) parts of the VNO in cross-section. A 40 × 40 µm grid is shown over the receptor zone of nuclei in a–d. Scale bars: a = 200 µm; b–d = 50 µm

mations were used in these cases. Ratios were converted using the arc-sine transformation and cell counts were converted using the square root transformation [18]. Since VNNE area and cell counts were measured multiple times within each VNO, these data were analyzed using a repeated measures 2-way ANOVA. Differences were considered significant at $P < 0.05$.

RESULTS

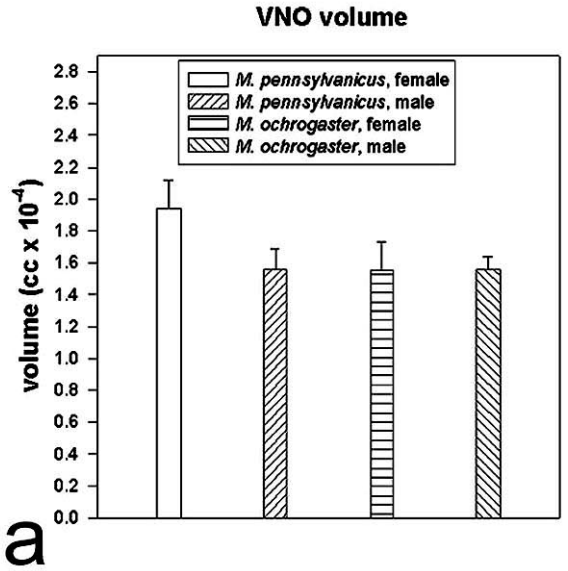
The VNNE was easily identified in all voles, exhibiting a contrasting thickness with the medial non-sensory, or receptor-free epithelium (Fig. 1). Anteroposteriorly, the vomeronasal neuroepithelial length was from 2.8 to 3.5 mm in *Microtus pennsylvanicus* and 2.7 to 3.8 mm in *M. ochrogaster*. The vomeronasal neuroepithelial volume ranged from 0.95 to 2.78 mm^3 in *M. pennsylvanicus* and 0.92 to 2.08 mm^3 in *M. ochrogaster*. Means and standard deviations of absolute VNO measurements are shown in Table 1 (replicated from [7]).

Results show significant ($P < 0.05$) differences in the palatal length between the species and within the species by sex interaction. In VNO size comparison, the only significant ($P < 0.05$) difference was found in the ratio of VNNEV to palatal length

Table 1
Descriptive statistics and analysis of variance (ANOVA) of palatal length and vomeronasal organ (VNO) measurements

	M. pennyslvanicus mean (+/– std. dev.)		*M. ochrogaster* mean (+/– std. dev.)		F-values		
	Females	Males	Females	Males	Species	Sex	Species ×Sex
PL (mm)	14.20 § (0.56)	15.26 § (0.78)	14.23 (1.14)	13.87 (0.47)	5.89*	1.51 ns	6.48*
VNNEL (μm)	3.21 (0.20)	3.20 (0.26)	3.14 (0.39)	3.16 (0.21)	0.31 ns	0.0001 ns	0.02 ns
VNNEV ($cc \times 10^{-4}$)	1.94 (0.50)	1.56 (0.29)	1.55 (0.44)	1.56 (0.22)	1.85 ns	1.74 ns	1.83 ns
VNNEL/PL	0.23 (0.01)	0.21 (0.02)	0.22 (0.03)	0.23 0.02)	0.85 ns	0.43 ns	2.02 ns
CrVNNEV/PL	0.0041 § (0.0004)	0.0035 § (0.0004)	0.0038 (0.0004)	0.0039 (0.0003)	0.12 ns	3.06 ns	5.55*

PL = palatal length; VNNEL = vomeronasal neuroepithelium length; VNNEV = vomeronasal neuroepithelium volume; CrVNNEV/PL = cube root of VNNEV/PL; § = paired means that were significantly ($P < 0.05$) different from each other; * = significant difference, p-value < 0.05; ns = no significant difference, p-value > 0.05


VNO volume
M. pennsylvanicus, female
M. pennsylvanicus, male
M. ochrogaster, female
M. ochrogaster, male
volume (cc x 10-4)
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
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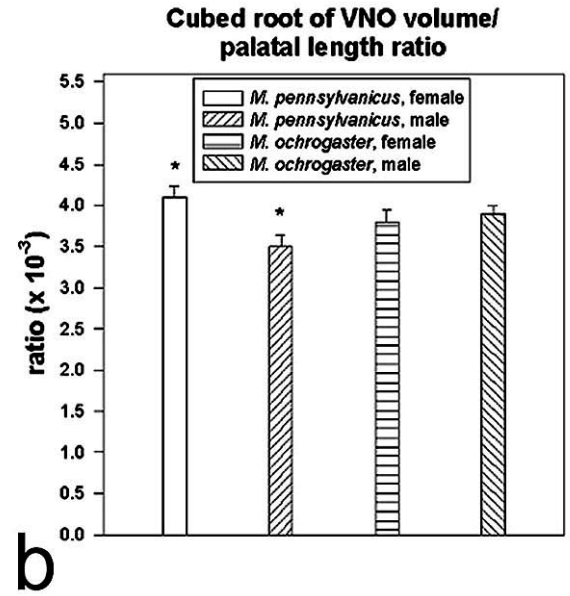
Cubed root of VNO volume/
palatal length ratio
M. pennsylvanicus, female
M. pennsylvanicus, male
M. ochrogaster, female
M. ochrogaster, male
ratio (x 10-3)
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
*
*
b

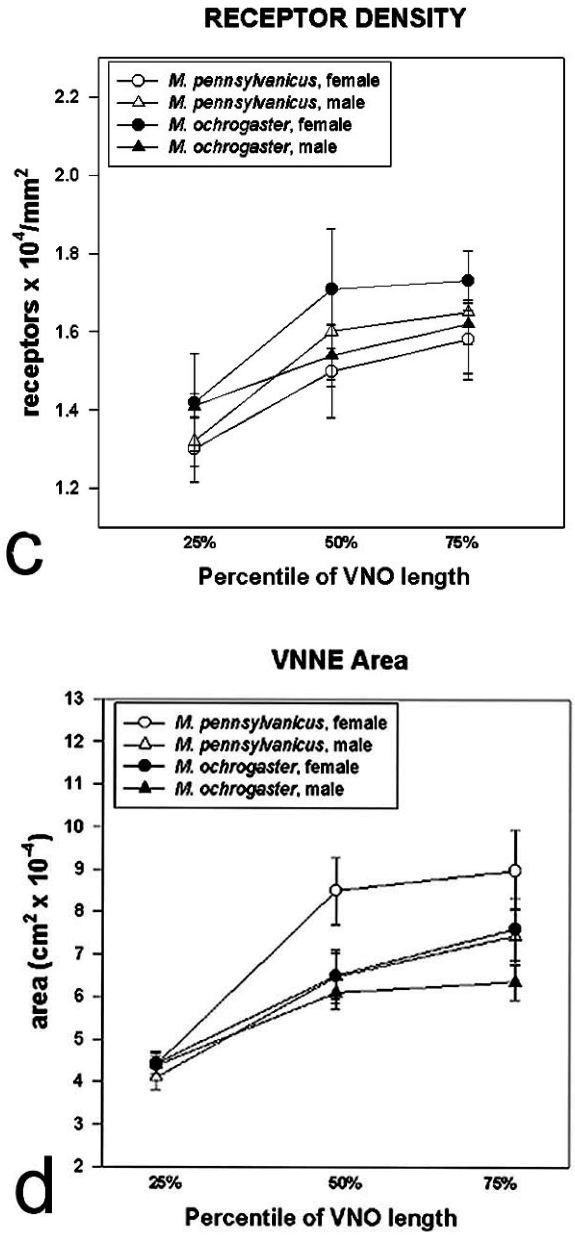

Fig. 2. Graphs showing the comparison between VNO volume (a), VNO volume/palatal length ratio (b), receptor density (c) and VNNE area (d) between species and sexes. Note that the greatest contrast occurs between female and male *M. pennsylvanicus* in VNNE volume and area (female > male). * = means significantly different at $P < 0.05$

(VNNEV/PL). No significant differences ($P > 0.05$) were noted in the analysis of absolute VNNE length or volume (Figs 2a, b). Results also revealed no significant ($P > 0.05$) differences between the two species, the sexes, and sex by species interaction in absolute or proportional measures of VNNE size. *Post hoc* Student's *t*-tests revealed that significant ($P < 0.05$) differences existed in palatal length and VNNEV/PL ratio between sexes of *M. pennsylvanicus* but not between sexes in *M. ochrogaster*.

Means and standard deviations of receptor cell counts are shown in Table 2 along with an analysis of variance at the three percentiles. Results showed no significant

Table 2
Descriptive statistics and repeated measures 2-way analysis of variance (ANOVA) of receptor cell count (# per mm^2) at the 3 different percentiles

	M. pennyslvanicus mean (+/– std. dev.)		*M. ochrogaster* mean (+/– std. dev.)		F-values		
	Females	Males	Females	Males	Species	Sex	Species ×Sex
25th percentile	1.30×10^4 ($0.22\times10^{4)}$	1.32×10^4 (0.14×10^4)	1.42×10^4 (0.28×10^4)	1.41×10^4 (0.08×10^4)	0.008 ns	1.04 ns	0.85 ns
50th percentile	1.49×10^4 (0.31×10^4)	1.60×10^4 (0.27×10^4)	1.71×10^4 (0.34×10^4)	1.54×10^4 (0.21×10^4)			
75th percentile	1.58×10^4 (0.27×10^4)	1.65×10^4 (0.35×10^4)	1.73×10^4 (0.17×10^4)	1.62×10^4 (0.14×10^4)			

ns = no significant difference; p-value > 0.05

Table 3
Descriptive statistics and repeated measures 2-way analysis of variance (ANOVA) of VNO neuroepithelial area (in cm^2) at the 3 different percentiles

	M. pennyslvanicus mean (+/– std. dev.)		*M. ochrogaster* mean (+/– std. dev.)		F-values		
	Females	Males	Females	Males	Species	Sex	Species ×Sex
25th percentile	4.64×10^{-4} (0.82×10^{-4})	3.80×10^{-4} (1.0×10^{-4})	4.42×10^{-4} (0.56×10^{-4})	4.39×10^{-4} (0.64×10^{-4})	0.208 ns	4.37*	0.534 ns
50th percentile	8.65×10^{-4} (0.24×10^{-4})	6.45×10^{-4} (1.66×10^{-4})	6.50×10^{-4} (1.21×10^{-4})	6.09×10^{-4} (1.01×10^{-4})			
75th percentile	8.94×10^{-4} (0.29×10^{-4})	7.44×10^{-4} (1.69×10^{-4})	8.08×10^{-4} (1.53×10^{-4})	7.44×10^{-4} (1.69×10^{-4})			

* = significant difference, p-value < 0.05; ns = no significant difference, p-value > 0.05

($P > 0.05$) differences at any of the three selected VNO sections between the species, the sexes, or sex by species interaction. Analysis of VNNE area (Table 3) revealed no significant ($P > 0.05$) differences in main effects of species or species X sex interaction, but a significant main effect of sex. Graphically (Fig. 2d) this appeared to be due primarily to larger VNNE area in the caudal one-half of *M. pennsylvanicus* females. In general, graphs suggested an increasing receptor cell density and VNNE area towards the caudal section of the VNO length in all our groups (Figs 2c, d). A trend of increasing receptor cell density towards the caudal end of the VNOs was noted in all our groups (Figs 2a–d).

DISCUSSION

These results support our original finding [7, 17] that VNOs are not significantly different in size in wild *Microtus* species that vary in male parental tendencies. However, the present study does indicate that sexual dimorphism is significantly greater in the species exhibiting more disparate parental tendencies. In particular, the results herein support our preliminary findings that female *M. pennsylvanicus* have larger VNOs than conspecific males [7]. In our preliminary study [7], we debated the importance of proportional as opposed to absolute differences in VNNE volume (see Table 1). The present study provided more detailed information on *M. pennsylvanicus*, revealing significant sex differences in absolute measurements of VNNE area (female > male) but no significant differences in receptor neuron density. Thus, regardless of the validity of correcting for body size when making intraspecific comparisons of VNO size, females appeared to have some significantly larger VNO measurements than males (both proportionally and absolutely).

Figure 2 qualitatively indicates that the main effect of sex was primarily due to large VNNE in the caudal half of the VNOs of female *M. pennsylvanicus*. Studies that have attempted to characterize evolutionary influences on VNO size in vertebrates primarily have discussed males [1, 14]. This is not surprising since the direction of VNO dimorphism has been reported as male > female in all reports, until the present study. Behavioral correlates of VNO removal or nerve lesions in females have some general similarities to those of males (aggression, mate preference), but are contextually unique. We hypothesize that the larger VNOs of female *M. pennsylvanicus* relate most strongly to mate selectivity and/or maternal aggression. The mechanisms that affect these behaviors are not generalized in rodents. Induction of estrus appears to be strongly linked to vomeronasal function in *M. ochrogaster* [5, 23], but not in *M. pennsylvanicus* [8]. Maternal aggression is strongly linked to vomeronasal function in mice [2, 24], but not in rats, which rely on olfactory function [4]. There is insufficient research regarding VNO/olfactory mediation of maternal aggression in voles. It is possible that an increased role in maternal aggression may be correlated with increased VNO size in female voles. VNO size could be under high selective pressure in females of promiscuous species that rear offspring alone. The enlarged VNO of female *M. pennsylvanicus* can then be viewed as an

investment in indirect parental behavior (such as nest guarding). Behaviorally, monogamous vole mothers spend significantly more time exhibiting direct parental care than the promiscuous ones [19]. Furthermore, the infanticidal tendencies may be greater in male *M. pennsylvanicus* [20] compared to male *M. ochrogaster* [6], so understanding the role of the VNO in maternal aggression is particularly interesting in this species. It also will be of great interest to know whether seasonal variations occur regarding VNO dimorphism in *M. pennsylvanicus*. The data of the present study are derived from females that were all pregnant or exhibited corpora lutea.

Certain common patterns of receptor distribution are interesting in comparison to data presented on other mammal species by Weiler et al. [21, 22], who found that cross-sectional neuroepithelial area of the VNO was relatively stable rostrocaudally in ferrets, whereas in rats, area was greater in the caudal half of the VNO. Thus, a similarity may exist among rodents in a greater receptor density and cross-sectional area toward the caudal one-half of the VNO. This may indicate that chemostimuli are preferentially analyzed within the caudal portion of the VNO, placing a unique emphasis on the vasomotor pump mechanism in these mammals [9]. Weiler et al. [21] also considered the ferret VNO to be rudimentary, although it possessed a neuroepithelium. Nonetheless, it may be that better developed VNOs exhibit more neuroepithelium caudally.

As mentioned earlier, other VNO studies have been conducted on laboratory-bred animals. Given the multitude of environmental factors that are left uncontrolled in the study of wild-caught animals, it may be remarkable that significant differences were detected. Although our previous work [7] detected no significant VNO differences between pregnant and non-pregnant females, it is probable that these populations were in a period of intense reproductive activity; the importance, if any, of cyclical endocrine changes on female VNO size is unknown. Furthermore, factors such as pheromones, which are important in reproductive behavior and reproductive status (e.g., [12]), can be more easily controlled in laboratory settings than in the field. Our data suggest that the relationship between VNO function and female behavior merits further investigation using experimental protocols in the laboratory setting, particularly using *Microtus pennsylvanicus*.

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