Changes in Social Interaction Adolescent Male Giraffes (Giraffa Camelopardalis) as they Shift from a Social to Solitary Lifestyle

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ABSTRACT

Social interactions that result in preferential relationships between individuals have been observed in multiple species of mammals. Female mammals tend to stay in long-term associations with other females, while males rarely maintain such interactions once they reach sexual maturity. For example, adolescent male giraffes (Giraffa camelopardalis) form bachelor herds in the wild and shift to a solitary lifestyle when they reach adulthood. Males in bachelor herds engage in social interactions and display preference and avoidance behaviors toward one another, indicating the establishment of individual-specific preferences. However, the process by which male giraffes’ transition from a social lifestyle as adolescents to a solitary existence as sexually mature adults is poorly understood. To understand this process, the frequency of social behavioral displays in a captive population of male giraffes at the Naples Zoo in southern Florida was examined as they transitioned from immature adolescence into adulthood. Younger male giraffes spent more time in close proximity to each other than did older males. While younger and older male giraffes showed similar frequencies of social behavioral displays, the types of behaviors that the males displayed changed with age. Younger males showed more contact interactions, such as neck bumping, while older males showed more sexual interactions and body examinations, such as mounting and anogenital exam. The amount of urine examinations remained constant, suggesting it was consistently observed throughout all ages. These results suggest that male giraffes change the type of social behavioral displays, consistent with their transition from a social to solitary lifestyle; older animals begin to separate and show agonistic behavioral patterns consistent with the formation of a dominance hierarchy and isolation.

INTRODUCTION

A wide variety of species show social behavioral displays and preferential relationships (Bashaw et al. 2007). Among mammals, females frequently form herds composed of related and unrelated females that work together to support and increase their offspring’s chances of survival, e.g., African lion (Panthera leo) (Packer et al. 1987), the greater spear-nosed bat (Phyllostomus hastatus) (McCranek et al. 1981), and the spotted hyena (Crocuta crocuta) (Tilson et al. 1984). For example, herds of female African elephants (Loxodonta africana) increase the chances of survivability of related or unrelated calves by remaining together (Lee et al. 2016).

While females commonly form and stay within stable herds throughout their lives, mammalian males tend to join fission-fusion networks with other males during adolescence (e.g., bachelor herds). These bachelor herds develop for a variety of reasons, including the transmission of social and ecological knowledge, protection from predators, and development of mating and fighting skills (Berchovitch et al. 2006; Grinnell et al. 1995; Richard et al. 2013). For example, bachelor herds form naturally in the wild among impala (Aepyceros melampus) (Averbeck et al. 2010), white-faced capuchins (Cebus capuchinus) (Perry 1998), and bighorn rams (Ovis canadensis nelson) (Hass et al. 1991). Mountain gorillas (Gorilla beringei beringei) form all-male adolescent groups to gain protection when displaced from family units by older, dominant males (Robbins 2010). Within these groups, male gorillas show homosexual displays towards one another, where displays appear to help males develop socially in the absence of females (Robbins 2010). In pronghorns antelopes, (Antilocapra americana ord), males in bachelor herds tend to interact more with same age/size males than with other males (Kitchen 1974). For example, yearling males (aged 1-2) show more interactions between other yearlings than with adult bulls and any interaction between yearlings and adult bulls tends to be short-lived (Kitchen 1974). While the amount of interactions decline with age, older male pronghorns interact with each other for longer periods of time and show the formation of a dominance hierarchy that can lead to territoriality (Kitchen 1974).

Male giraffes are known to form bachelor herds during adolescence, where they engage in social behavioral displays before shifting to a solitary lifestyle as adults (Bercovitch et al. 2014). Males will reach adolescence between one and two years of age, the time when calves stop nursing from their mother, and will generally reach sexual maturity between the ages of eight and nine (Bercovitch et al. 2010; Pratt et al. 1982). This study examined the social behavioral displays among a small bachelor herd of adolescent male giraffes at different stages during their development. Giraffes would be expected to change the amount and types of behaviors displayed during the shift from their social to solitary life histories if they showed similar developmental changes as pronghorns. For example, older males were predicted to become less social and display more agonistic interactions than younger animals as they aged.
METHODS
Subjects and Study Site
The study was conducted with an all-male giraffe herd residing in the Naples Zoo at Caribbean Gardens in Naples, FL. During the 2013 portion of the study, seven adolescent male giraffes were studied. Their ages ranged between three and four, and they had all lived in the enclosure for over a year before the start of the study. In 2017, five of the original male giraffes (aged seven to eight years) were observed for a second time to compare how social behavioral displays changed as animals matured. Two giraffes from the 2013 study had been relocated from the zoo prior to starting the second half of the study.

The study was conducted with an all-male giraffe herd residing in the Naples Zoo at Caribbean Gardens in Naples, FL. Eight giraffes were studied. Their ages ranged between three and four, and they had all lived in the enclosure for over a year before the start of the study. In 2017, five of the original male giraffes (aged seven to eight years) were observed for a second time to compare how social behavioral displays changed as animals matured. Two giraffes from the 2013 study had been relocated from the zoo prior to starting the second half of the study.

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The enclosure consisted of three separate areas that could be connected or separated, allowing the giraffes free access to each part of the enclosure (Figure 1). During the 2013 study, giraffes were held in a night enclosure (approximately 660 m²) between the hours of 15:30-10:00 the next morning. During the day, giraffes were moved into the day enclosure (approximately 1030 m²). In 2017, giraffes had access to both the night and day enclosure at all times.

Data Collection
Data were only collected when all of giraffes had access to each other (i.e., enclosure doors did not separate males from each other) and were not interacting with the zoo staff. For example, if a giraffe participated in a training session with the staff, data collection was stopped and continued only after all giraffes were together and not involved in training. Data were collected during the same time that the public had access to the viewing area (10:00 – 15:30 hours) because giraffes would be habituated to people, including the researchers. Data collection from this location and during this time also ensured unobstructed visual access to all sections of the enclosure. In 2013, this was the period of time giraffes had access to each other within the day enclosure before being moved to the night enclosure. The 2017 portion of the study used the same time frame to prevent any discrepancies that may have emerged because of daily cycles in behavioral patterns. In both 2013 and 2017, data were not collected between 13:00-13:25 when an educational keeper gave a talk to visitors that involved interacting and training with the giraffes. Data collection only resumed when criteria were met, i.e., males were not interacting with keepers and all males had access to each other.

In 2013, the seven giraffes were observed over 55 days, totaling 96 hours. In 2017, the five remaining giraffes were observed over 35 days, totaling 44 hours. Individual giraffes were observed during 15-minute focal-animal observations, where the frequencies of 15 social behavioral displays were recorded (Table 1). Data were collected on a pocket PC with the software Pocket Observer 3.0. These data were later quantified with The Observer XT 10.0. The order in which each individual giraffe was observed was randomized to prevent any order bias in the data collection.

Data Analysis
Data analyses were double blind to prevent bias. Analyses were conducted by CWG without knowledge of the focal animals that TR and SB observed during the 15-minute observation periods.

Table 1: List of all behaviors that were documented during the study.

| Behavioral Interactions | Definitions                      |
|-------------------------|----------------------------------|
| Anogenital Examination  | Actor giraffe licked or sniffed the recipient giraffe’s anogenital area. |
| Approach                | Actor giraffe moved towards the recipient giraffe, while the recipient giraffe was stationary. This behavior began when the actor became social (within one neck length away) or made contact with the recipient. |
| Attempted               | Actor giraffe attempted to lift its front legs and chest to rest it on top of the recipient giraffe’s posterior end, however failed to make complete contact with the rest of the recipient giraffe. |
| Mount                   | Actor giraffe hit or pushed its body against the recipient giraffe. |
| Body Bump               | Actor giraffe's penis was visible, while socially interacting with the recipient giraffe. |
| Erection                | Actor giraffe lifted its upper lips, while flaring nostrils. |
| Flehmen                 | Actor giraffe moved towards the recipient giraffe, while the recipient was walking away from the actor (both giraffes remained within one neck length away) |
| Follow                  | Actor giraffe moved towards the recipient giraffe, while the recipient was walking away from the actor (both giraffes remained within one neck length away) |
| Head Rub                | Actor giraffe rubbed its head on any part of the recipient giraffe’s body, except for the head and neck |
| Mount                   | Actor giraffe lifted its front legs and chest and rested it on top of the recipient giraffe’s posterior end. |
| Muzzle                  | Actor giraffe sniffed, licked, or rubbed, its head on the recipient giraffe’s head. |
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| Neck bump               | Actor giraffe stood parallel or facing recipient giraffe and swung its head and neck towards the recipient giraffe’s body, neck, or head, making contact. |
| Necking                 | Actor giraffe rubbed or intertwined its neck with the recipient giraffe’s neck. |
| Position                | Standing behind, the actor giraffe used its head, neck, chest, and/or legs to move the recipient giraffe directly in front of it. |
| Social Exam             | Actor giraffe licked or sniffed the recipient giraffe’s body, except head, neck, and anogenital area. |
| Urine                   | Actor giraffe licked the urine of the recipient giraffe. |
| Testing                 | This behavior could have occurred independently from ‘flehmen’ or ‘anogenital exam’. |

Figure 1: An overview of the giraffe enclosure at Naples Zoo at Caribbean Gardens in Naples, FL. Shown are the three different areas marked off by fencing. Shade cloths are hung in the day enclosure and over the public viewing area.
Prior to running a maximum analysis, the behavioral categories of mount, attempt mount, and erection were combined and categorized as “homosexual” as each behavior consisted of an intraspecific sexual display. A maximum likelihood factor analysis test was then run to identify latent variables (i.e., factors) of the recorded behavioral traits (Richards et al. 2013), i.e., anogenital exam, approach, body bump, flehmen, follow, head rub, homosexual, muzzle-muzzle, neck bump, position, social exam, and urine test (Table 1). Determining the number of described latent variables from the factor analysis was based on two considerations: 1) each recorded behavioral trait loaded strongly with at least one factor and 2) the eigenvalue was greater than 1 for all reported factors in a model. Once the number of factors was determined, loadings greater than 0.5 or less than -0.5 for any behavioral trait within a factor were identified as significant (Gunnels 2007). A qualitative description of the factor was then described based on the relationship among the associated behavioral traits. To determine whether identified latent variables changed over time, loadings associated with each of the described factors were regressed to calculate a single number that represented the expression of each latent variable for that animal during that observation (Gunnels 2007). The maximum likelihood factor analysis was calculated and loadings of latent variables were regressed using the statistical software R (Team 2013) within the package “psych” (Pratt et al. 1982).

Fisher-Pitmann Tests
To compare the expression of latent variables between adolescent (3-4 years old) and adult (7-8 years old) giraffes, we used one-way Fisher-Pitmann Tests based on 10,000 iterations were used (Neuhäuser et al. 2004). These tests were done using the “coin” package in R (Hothorn et al. 2006). Significant differences were identified for α < 0.05. Graphs were created in the package “ggplot2” in R (Wickham 2009).

RESULTS
Maximum Likelihood Factor Analysis
Two-factor, three-factor, or five-factor analyses did not provide an accurate description of the analyzed behavioral traits (Table 2). The four-factor maximum likelihood factor analysis was found to be the best fit for the data, explaining 59% of the variation between the two age groups (Table 3). The first factor, named “Sexual Interactions”, had positive loadings for position, homosexual, body bump, and follow. “Sexual Interactions” described 16% of the total variation (eigenvalue = 2.05). Necking, muzzle-muzzle, body bump and neck bump loaded positively for the second factor, named “Contact Interactions”, and explained 16% of the total variance (eigenvalue = 2.05). The third factor, named “Body Examine”, received positive loadings from anogenital exam, social exam, follow, and approach and described 15% of the total variance (eigenvalue = 1.99). Factor four, named “Urine Examination”, received positive loadings from urine test and flehmen; it made up the remaining 12% of the total explained variation (eigenvalue = 1.58). One behavioral trait did not load onto any factor; the loadings for head rub were all between -0.5 and 0.5 for each of the four identified factors.

Table 3: The table shows results of the best-fit maximum likelihood factor analysis. Factors were categorized by behavior loadings of >-0.5 or 0.5 <. Factors were then renamed based on the relationship of the identified behaviors. Head rub was the only behavior that did not load into any of the factors. Erection, Mount, and Attempt Mount were categorized as “Homosexual” before the maximum likelihood factor analysis was run.

Comparing Younger and Older Males
The percent of time that younger and older males spent in social proximity (i.e., one neck length away from another giraffe) differed (Figure 2: Z = -2.6178, P-value = 0.0086). Younger males spent 22.5% more time in close proximity to another animal than older giraffes. However, younger and older male giraffes displayed a similar number of social behavioral displays (Figure 3: Z = 1.2416, P-value = 0.2253). On average, younger males showed 11.6 social behavioral displays and older giraffes showed 14.3 displays per 15-minute observation.

Younger males showed contact interactions (i.e., Factor 2) more than older males (Figure 4a: Z = 3.747, p < 0.001). Older males showed sexual interactions (i.e., Factor 1) significantly more than younger males (Figure 4b: Z = 3.109, p < 0.001). In addition, older males showed body examination behaviors (i.e., Factor 3) significantly more than younger males (Figure 4c: Z = -3.603, p < 0.001). The frequencies of urine examinations (i.e. Factor 4) were not significantly different (Figure 4d: Z = 1.105, P-value = 0.273). Younger and older adolescent males performed similar amounts of urine examinations throughout the study.
Table 2: A two-factor analysis excluded 5 behaviors that failed to load into a factor and explained only 39% of the total variance. The three-factor analysis excluded three behaviors and explained only 50% of the total variance. The five-factor analysis excluded one behavior from fitting into one of the factors and explained 64% of the total variance. However, the five-factor analysis was not used because one of the identified factors provided a poor representation of the overall model; body bump loaded individually into the fifth factor and explained only 7% of the total variation (eigenvalue = 0.94).

Figure 2: The graph compares the amount of time younger males (aged three-four) and older males (aged seven-eight) spent in social proximity to one another during data collection (i.e. one neck length away from another giraffe).

In the box plots, the thick black lines represent medians, with the boxes showing the inner quartile range (25th to 75th percentiles), and the vertical lines represent 1.5 times the inner quartile range. Individual dots show measured data, including statistical outliers that are found beyond the vertical lines.

Figure 3: The graph compares the frequency of behaviors between young male giraffes (aged three-four) to their older selves (aged seven-eight). This graph describes the relationship between all of the behavioral displays (homosexual, position, follow, body bump, anogenital exam, social exam, approach, body bump, neck bump, muzzle, necking, flehmen, and urine test).

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Figure 4: The graph compares the frequency of four latent variables (i.e., factors) that described the underlying relationship of 15 behavioral displays shown by a captive population of adolescent males giraffes (aged...
three-four relative to their older selves aged seven-eight) at the Naples Zoo, FL: A) contact interactions (Factor 2), B) sexual interactions (Factor 1), C) body examine (Factor 3), and D) urine examine (Factor 4).

In the box plots, the thick black lines represent medians, with the boxes showing the inner quartile range (25th to 75th percentiles), and the vertical lines represent 1.5 times the inner quartile range. Individual dots show measured data, including statistical outliers that are found beyond the vertical lines.

**DISCUSSION**

While female giraffes tend to form stable herds with related and unrelated females that they maintain throughout their lifetime, the lifestyle of male giraffes changes with age (Bercovitch et al. 2013; Carter et al. 2013; Pratt et al. 1985). Nursing males remain with their mothers before moving to bachelor herds between the ages of one and two, where they socialize with other young male giraffes in all-male bachelor herds (Bercovitch et al. 2010; Pratt et al. 1982). As males reach sexual maturity, they shift from a social life in a bachelor herd to a more solitary lifestyle, where they only interact with other giraffes during reproduction. As a result, behaviors associated with different developmental stages would be expected to change as males mature similar to what has been observed among pronghorn males (Kitchen 1974).

In the context of this study, behavioral patterns of adolescent captive male giraffes within a bachelor herd changed with age. Younger males spent 22.5% more time in close proximity to each other than did older males, where close proximity could promote the formation of temporary relationships during this period of development. This finding was consistent with the observation that younger males in bachelor herds show preferences and avoidances towards one another (Richards et al. 2013). The observation that older males spent less time in social proximity was also consistent with their shift from a social to solitary lifestyle, where these older males could have begun to separate as fully reproductive adults (Le Pendu et al. 2000; Leuthold 1979; Pratt et al. 1982).

Younger males may have spent more time in social proximity than older males due to the two additional males included in the 2013 bachelor herd and a respectively smaller study site. This limited spacing could have prevented animals from separating from each other. However, if limited space and the number of animals in the bachelor herd explained the fact that younger males spent more time in close proximity, we should have also observed more social behavioral displays among these young males, where a larger number of animals in a more confined space would have been expected to create more opportunities to interact. This pattern was not observed. Instead, frequencies of social behavioral displays were similar between both age groups. Even though the 2017 bachelor herd had fewer animals that occupied a respectively larger area, older males showed the same amount of social behavioral displays as the younger males who interacted in a larger herd in a smaller space.

While the amount of social behavioral displays was similar across ages, the type of displays that males expressed towards each other changed with age. Younger males displayed more contact interactions. For example, these younger males showed a higher frequency of neck and body bumps as well as behaviors where their heads and necks intertwined. The higher frequency of contact interactions among younger males may have reflected the role of play and practice among young animals. Play promotes increased socialization of the young males while also providing practice for useful activities they may partake in as adults (Le Pendu et al. 2000; Pratt et al. 1985); contract interactions, such as repeated body and neck bumps, are not associated with dominance and/or submission behaviors in giraffes at this age (Le Pendu et al. 2000; Leuthold 1979; Pratt et al. 1985; Richards et al. 2013). Contact interactions were observed less frequently in older males. However, these behaviors appeared to be associated with the formation of a dominance hierarchy as males’ age (Kitchen 1974; Pratt et al. 1985).

While younger males showed more contact interactions, older males showed more sexual interactions, including homosexual displays. An increase in sexual interactions among the older male giraffes was consistent with a shift to sexual maturity and a solitary life (Pratt et al. 1985). If a dominance hierarchy were forming within the bachelor herd in this study, an increase in contact interactions among older males would be expected. By separating from other males to become more solitary, adult male giraffes could decrease competitive interactions that take place during reproduction. In addition, these behavioral changes could be the result of unidentified physiological changes that occur as males’ age; differences in gene expression as male giraffes reach sexual maturity could attribute to hormonal shifts and behavioral changes. Such developmental changes also occur in other species. For example, genomic and endocrinological changes occur in insect species, such as honeybees, that shift from nurses to foragers as they age (Ueno et al. 2015). However, these changes occur in female honeybees, not males. Research is still needed to identify if changes in behavior as male ungulates mature is related to endocrinological changes.

Older males also showed more “body examines”, such as anogenital and social exams. In ungulates, a male usually performs anogenital examinations during courtship. This may be consistent with the shift to a solitary lifestyle as they prepare to enter the reproductive stage of their life. Social exams could in turn be classified as forms of communication. Giraffe communication is poorly understood due the ambiguity of the data collected thus far. The interpretations made on giraffe communication are primarily based on data that has been collected through opportunistic observation and is broadly grouped as visual, olfactory, and auditory (Kasozi et al. 2018). As the males have been in contact with each other over multiple years, they may be able to identify one another through these interactions. There is little research on male-male examinations and more research would be needed to determine the function of the examination.

Male giraffes raised in a captive bachelor herd environment still undergo the same lifestyle shifts that wild
males do; a captive bachelor herd proved to show the shift from adolescence to adulthood is through behavioral changes. As the males aged, older males became less social but displayed an equivalent amount of behavioral displays. Older males also showed less contact interactions and more sexual interactions and body examines. More research needs to be done to fully understand what causes the behavioral changes adolescent male giraffes undergo as they shift from a social to solitary existence.

Understanding the social lifestyle of male giraffes during adolescences and adulthood is information that will ensure the welfare of future captive male giraffe bachelor herds in zoos and other facilities. Ultimately, it will be important to understand and observe how captive adult male giraffes will behave as they continuously move forward in their solitary lifestyle in an environment where they cannot be alone.

REFERENCES
Averbeck, C., et al. Hunting Differentially Affects Mixed-Sex and Bachelor-Herds in a Gregarious Ungulate, the Impala (Aepyceros melampus: Bovidae). African Journal of Ecology 48.1 (2010): 255-264.
Bashaw, M. J., et al. The Structure of Social Relationships Among Captive Female Giraffe (Giraffa camelopardalis). Journal of Comparative Psychology 121.1 (2007): 46.
Bercovitch, F. B., et al. Sociosexual Behavior, Male Mating Tactics, and the Reproductive Cycle of Giraffe (Giraffa camelopardalis). Hormones and Behavior 50. 2 (2006): 312.
Bercovitch, F. B., et al. Ecological Determinants of Herd Size in the Thornicroft’s Giraffe of Zambia. African Journal of Ecology 48. 4 (2010): 962-971.
Bercovitch, F. B., et al. Herd Composition, Kinship and Fission–Fusion Social Dynamics Among Wild Giraffe. African Journal of Ecology 51. 2 (2013): 206-216.
Bercovitch, F. B., et al. The Composition and Function of All-Male Herds of Thornicrofts Giraffe, Giraffa camelopardalis thronicrofti, in Zambia. African Journal of Ecology 53. 2 (2014): 167-174.
Carter, K. D., et al. Social Networks, Long-Term Associations and Age-Related Sociability of Wild Giraffes. Animal Behaviour 86. 5 (2013): 901-910.
Grinnell, J., et al. Cooperation in Male Lions: Kinship, Reciprocity or Mutualism? Animal Behaviour 49. 1 (1995): 95-105.
Gunellus IV, C. W. Seasonally Variable Eusocially Selected Traits in the Paper Wasp, Mischocyttaridns mexicanus. Ethology 113.7 (2007) 648-660.
Hass, C. C., et al. Structure and Ontogeny of Dominance Relationships among Bighorn Rams. Canadian Journal of Zoology 69. 2 (1991): 471-476.
Horoza, E., et al. The First Description of Dominance Hierarchy in Captive Giraffe: Not Loose and Egalitarian, but Clear and Linear. PloS One 10. 5 (2015)
Hothorn, T., et al. A Lego System for Conditional Inference. The American Statistician 60. 3 (2006): 257-263.
Kasozi, H., et al. How do Giraffes Locate One Another? A Review of Visual, Auditory, and Olfactory Communication Among Giraffes. Journal of Zoology (2018)
Kitchen, D. W. Social Behavior and Ecology of the Pronghorn. Wildlife Monographs 38 (1974) 3-96.
Lee, P. C., et al. The Reproductive Advantages of a Long Life: Longevity and Senescence in Wild Female African Elephants. Behavioral Ecology and Sociobiology 70. 3 (2016): 337-345.
Le Pendu, Y., et al. The Social Organization of Giraffes in Niger. African Journal of Ecology 38. 1 (2000): 78-85.
Leuthold, B. M. Social Organization and Behavior of Giraffe in Tsavo East National Park. African Journal of Ecology 17. 1 (1979): 19-34.
McCraken, G. F., et al. Social Organization and Kinship in the Polygynous Bat Phyllostomus hastatus. Behavioral Ecology and Sociobiology 8. 1 (1981): 11-34.
Neuhäuser, M., et al. The Fisher-Pitman Permutation Test when Testing for Differences in Mean and Variance. Psychological reports 94. 1 (2004): 189-194.
Packer, C., et al. Intrasexual Cooperation and the Sex Ratio in African Lions. The American Naturalist 130. 4 (1987): 636-642.
Perry, S. Male-Male Social Relationships in Wild White-Faced Capuchins, Cebus capucinus. Behavior 135. 2 (1998): 139-172.
Pratt, David M., et al. Population, Distribution, and Behavior of Giraffe in the Arusha National Park, Tanzania. Journal of Natural History 16. 4 (1982): 481-489.
Pratt, D. M., et al. Giraffe Social Behavior. Journal of Natural History 19. 4 (1985): 771-781.
Richards, T., et al. Preferences Across Different Social Networks Among Captive Adolescent Male Giraffe (Giraffa camelopardalis). (2013)
Robbins, M. M. Male-Male Interactions in Heterosexual and All-Male Wild Mountain Gorilla Groups. Ethology 102. 7 (2010): 942-965.
Team, R. Core. R: A Language and Environment for Statistical Computing. (2013): 201.
Tilson, R. L., et al. Social Dominance and Feeding Patterns of Spotted Hyenas. Animal Behavior 32. 3 (1984): 615-724.
Wickham, H. ggplot2: Elegant Graphics for Data Analysis Springer-Verlag New York. (2009)
Ueno, T., et al. Changes in the Gene Expression Profiles of the Hypopharyngeal Gland of Worker Honeybees in Association with Worker Behavior and Hormonal Factors. PloS One 10. 6 (2015): e0130206.