Variability of Sexual Dimorphism in Minnesota Mustelids

Mayer, Treana. University of Minnesota – Twin Cities
Undergraduate Research Opportunities Program Student Researcher
Advisor Dr. Sharon Jansa

July 2015

Abstract

Sexual dimorphism is a fascinating evolutionary phenomenon to explore in depth, particularly within Carnivora and the family Mustelidae. Previous findings show high instances of dimorphism within these taxanomic groupings (Gittleman 1997), and in some instances the degree of dimorphism may be a short term responsive adaptation to environmental conditions (Powell 1997). It is then especially relevant to examine dimorphism in depth for populations living in temperate ecosystems likely to undergo drastic alteration due to climate change in the near future. This study on variability in dimorphism for Minnesotan Mustelids; with sexual selection and ecological pressure focuses on 4 select species found in Minnesota, namely *Mustela erminea, M. frenata, Neovison vison* and *Procyon lotor* serving as a control, with at least 5 specimens of each sex sampled for each species. Delving deeper into a geographically specific genus can reveal more information about the evolutionary and phylogenetic history for dimorphism in this area, and help to illuminate possibilities about the future of these populations as they face new challenges. The two main hypotheses for driving dimorphism are ecological niche separation and sexual selection (Gittleman 1997). In this study, differences in canine and carnassial teeth were compared, to find which of these driving forces was more prominent historically for the populations living in Minnesota; with dimorphic canines pointing to sexual selection and dimorphic carnassials indicating dietary specialization between the sexes. Many significant dentition and skull differences were found for half of the species examined, namely *M. erminea* and *N. vison*.

Introduction

Sexual dimorphism can vary from subtle to extreme differences in the physiology of the binary sexes in a given animal species, and the degree of differences helps to elucidate a fascinating aspect of that species' evolutionary history and environmental constraints over time. There are two major competing hypotheses for the underlying reasoning behind sexual dimorphism with differing evolutionary advantages for each one. The first of these hypotheses deals purely with sexual selection, in that females are choosy about selecting male mates who are more likely to produce viable offspring. On the other side of this story, males must compete with each other, often using a visual display for communicating their superiority over others. The limiting resource for females is producing high quality offspring, and the limiting resource for males is the opportunity to mate. The driving forces for this

hypothesis include an increased incidence of successful reproductions for males expressing this particular sex based phenotypic difference. For females there are varying advantages. Important and likely common advantage is the use of a dimorphic characteristic as an indicator for other genetic or physical quality that leads to increased rates of offspring survival.

The other main hypothesis of ecological niche separation doesn't involve the choice of mates directly and instead focuses on the survival of the adults with decreased competition among the sexes for food resources, although this does increase chances of reproduction in the future. In these instances dimorphism arises to better adapt males and females for cohabitating in a given area without driving the other towards starvation while competing for the same limited resources. This hypothesis can be considered more important for a species that faces greater limitations and stress on foraging, and less emphasis on offspring's adaptive survival against predators and other environmental constraints. Given this, it might follow that more species within Carnivora exhibiting sexual dimorphism would fall under the ecological niche hypothesis rather than the sexual selection hypothesis, as most carnivorous species in Carnivora are highly competitive amongst each other for food resources. The carnassials teeth are under dietary selective pressures due to their important functionality in carnivores' ability to acquire and process certain sized prey (Meiri 2005).

By examining the life history and ecology of specific mustelids, the seemingly more appropriate dimorphism hypothesis for each species may be conferred, after which each supposition will then be tested with an analysis of the significant differences, if any, of dentition morphology and skull size between the sexes. These results will be compared with what the literature presents on those species' instances of dimorphism or dietary specialization between the sexes.

Genus *Mustela, Neovison* and *Procyon*

The analysis of sexual dimorphism in carnivores by Gittleman and Valkenburgh suggests that the groupings mustelids, felids and procyonids have higher instances of sexual dimorphism in craniodental features than found in other families in Carnivora (1997). This additional analysis seeks to expound upon the findings for mustelids in particular and delve deeper into a species specific level. The life history, ecology and behavior that may be associated with dimorphism for each mustelid and procyonid analyzed in this paper are individually summarized below, although within *Mustela* there are many overlaps of breeding system and food preferences.

Mustela erminea, commonly known as the stoat, is a small weasel like mammal that hunts primarily small rodents, and occasionally rabbits if the stoat is large enough (Moors 2007). Its habitat includes most northern climates that experience severe winters and extended periods of snow cover (Powell 2006). This mustelid has been shown to exhibit marked dimorphism in size (Gittleman 1997), as well as dietary specialization between the sexes in certain localities but not all (Moors 2007). Important life history characteristics outlined in some of Powell and King's research regarding stoat dimorphism and ecological factors states that parental investment is unequal; males grow faster than females, and yet females reach sexual maturity a year earlier than males (Powell 1997). Evidence presented in the same article mentioned above suggests the incidences of dimorphism in stoats did not display short term responses to the environment rather than a long-term adaptation (1997). That study focused on stoat populations in Britain, whereas Minnesotan stoat populations having responded to different environmental constraints may exhibit different results. The life history variables regarding their breeding systems as presented in the literature suggests that sexual selection may be a stronger factor, and the instances of dietary specialization may be a by-product of their differences in size while males compete with one another for mate selection.

Mustela frenata, referred commonly as the long-tailed weasel, is the next mustelid to be considered. They are generally regarded as more elusive weasels for monitoring, although it is known that their ranges are restricted to America from approximately 50 degree north to 15 degrees south (King 1989). Their diets are considered more general than that of the stoat, and they also exhibit size differences between the sexes that result in dietary specialization; namely a female's ability to fit into small prairie vole burrows 64% more often than males (Moors 2007). Their breeding system, like most weasels, shows that there is little evidence of male parental care (Moors 2007). The long-tailed weasel is the largest of the Mustela genus (King 1989), which points to reduced degrees of dimorphism according to an analysis by P. Moors who found a negative correlating relationship between male weight and the ratio of weight dimorphism between the sexes for Mustelids (2007). This species also points towards sexually selected dimorphism over ecological niche separation.

Neovison vison, also known as the American Mink, was once a part of the *Mustela* genus but is now placed in *Neovison*. Phylogenetics suggest it is still closely related to *Mustela* and relevant for this study. This species is different from the other weasels being examined in that it is semi-aquatic. This seems to lead to slightly more intra-sex territory overlap, suggesting an explanation for the behaviors recorded by a radio-collared observational study by Zshille et al that addresses intra-species competition (Zschille 2010). According to that study, the differences in the behaviors of males and females has to do primarily with their hunting activities. In regards to their reproductive tactics, it is known that females mate with multiple males as a strategy to increase chances of fit offspring, and there have been observations of other forms of reproductive flexibility, with instances of breeding outside the usual season (Garcia 2010). The combined evidence makes a strong case for ecological niche separation to explain any possible dimorphism in *N. vison*.

Procyon lotor, the raccoon, is taxonomically placed in the sister taxa group to Mustelidae according to phylogenetic findings (Koepfli 2008). Their diets are one of the most flexible of the species compared in this study, being omnivorous and successful opportunistic scavengers (Johnson 1970). This leaves little pressure for ecological niche separation of the sexes when their ranges of utilizable food resources hardly become scarce enough to drive them to towards niche separation. Their mating and territoriality is more similar to those of the weasels, indicating that males defend territories for the privilege of mating rights with females who reside there (Fritzell 1978). This may suggest that if dimorphism is present, it would be due to sexual selection.

In summary, based on this literature review, sexual selection based dimorphism is hypothesized for *M. erminea, M. frenata,* and *P. lotor. N. vison* is the only species in this study with stronger evidence for the hypothesis of ecological niche based dimorphism based on their life history.

Given these hypotheses, it is important to view them from a historical evolutionary standpoint to analyze if this makes sense parsimoniously. In order to do so effectively, phylogenetic based groupings (**Figure 1**) gives the most information about genetic inheritance for analyzing the relatedness and lineage of traits. According to the most recent analysis of this taxanomic group, *N. vison* and *M. frenata* are sister species with relatively little divergence from one another in comparison to the rest of Mustelidae, and are also the only grouping with genetic evidence for descending from New World ancestors. *M. erminea* is sister taxa to many more Old World mustelids, and relatively removed from the other species included in this study. *P. lotor* is not included in this abridged tree, and is placed in the sister taxon to all other species in Mustelidae, the most evolutionarily removed from the mustelids included in this study. Assuming all have evidence for dimorphism, the least number of changes in the driving forces behind it would be 1 gain of sexual selection and 1 loss in the form of ecological niche

separation taking its place with the ancestor of *N. vison*. This would fall in line with the idea that

dimorphism evolved in a common ancestor for all of Carnivora (Gittleman 1997).

Figure 1:

Phylogenetic tree of *Mustela* according to multi-gene analysis, differentiated by geographic distribution.
Excerpt of the open access phylogenetic tree of Mustelidae created by Koepfli et al.
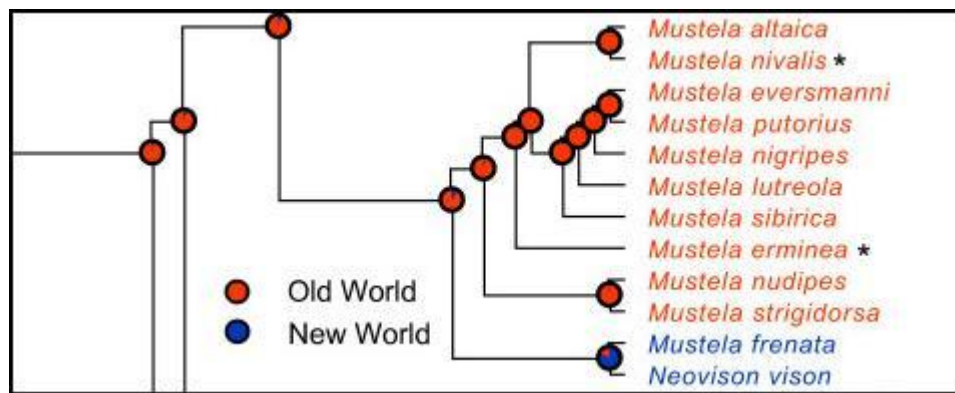
Methods

For the data collection of this exploratory analysis, samples were drawn from the Bell Museum's

research collections at the University of Minnesota, Twin Cities campus. All of the catalogued specimens

for the 4 species *Mustela erminea, M. frenata, Neovison vison,* and *Procyon lotor* were evaluated on a

scale from 1-3 for quality of dentition and skull. This first step eliminated inaccuracies in the

measurements due to natural wear, breakage and lost teeth. The specimens to be used for

measurements were randomly selected from the pool of high quality graded skulls, and without overlap

of exact retrieval locations to avoid morphological differences due to locality. The measurements were

taken by an electronic digital caliper in millimeters, and included the upper canine length and width, the

fourth upper premolar length and width, and overall skull length. Measurement for the canine used the

gumline marking of the tooth if it was noticeably receded. Width for the premolar was taken between the two outer edges of the two buccal side cusps of the tooth, and the length from the gumline to the tip of the middle cusp. The skull length used was the longest distance found between the rostrum and the occipital.

Analysis involved comparing the difference in means between the sex groups of each species to a randomization null distribution. That distribution was used to calculate a P-value for the sample's difference in means against the null hypothesis that there are no differences between the physiologies of the sexes. The randomization distribution was created by shuffling the sex category to break the potential relationship between the measurements and sex. P-values were calculated for each variable of each species and are summarized in **Table 1**.

Results

The summary of the results for this study are outlined in **Table 1**. The sample data were also plotted side by side to compare the spread of the data, and degree of overlap using their standard deviations and 95% confidence intervals. The threshold of 0.05 for significant p-values used in other similar analyses was used for determining significant differences.

Significant values were found for more than one category of differences in means for measurements taken from *M. erminea* and *N. vison.* This sample does not suggest evidence for dimorphism between the sexes for *M. frenata* and *P. lotor* in Minnesota*.

Table 1:

Species	CL	p-value	CW	p-value	PMW	p-value	PML	p-value	SL	p-value
				Measurements of differences in means (mm)						
Mustela erminea	1.41	<0.001	0.416	<0.001	0.669	0.002	0.287	<0.001	6.03	<0.001
Mustela frenata	0.308	0.137	1.44	0.01	0.416	0.122	0.331	0.154	3.12	0.13
Neovison vison	1.18	0.034	0.729	0.004	0.528	0.004	0.375	0.056	7.56	<0.001
Procyon lotor	0.176	0.411	0.885	0.015	0.0917	0.395	0.408	0.095	3.17	0.158

This table shows the sampled differences in means (male - female) for canine and fourth upper premolar lengths and widths, skull length, and associated p-values. CL is canine length, and CW is canine width. PMW represents premolar width, specifically the fourth upper premolar of the carnassial pair. PML is premolar length. SL represents skull length. All measurements are in units of millimeters.

Discussion

There is generally an agreement that due to the difficulty of testing for ecological causes for sexual dimorphism, and that it is often the less parsimonious option in comparison to the alternative; it is easier to consent to the idea that dimorphism is a long term genetic advantage for sexual selection. There have been many examples of ecological causation for dimorphism in foraging specialization between the sexes however, so it is important to investigate the possibility of ecological competition driving dimorphism in contrast to simply mate competition (Shine 2010). There are studies that explore the variability of sexual dimorphism in body size differing regionally (Moors 2007), and this study is a brief investigation in the variability of the sampled populations in Minnesota to compare with populations elsewhere. The results of this study are not easily explained by the most parsimonious lineage of dimorphism and the hypotheses gathered from general information in wider ranges of geographic regions. The significant results for *M. erminea* and *N. vison* had relatively equal levels of significance between the canines, premolars and skull length. This suggested whole body size difference

rather than either sexual selection for canine displays or for larger prey processing capacity of the carnassials. *M. frenata* and *P. lotor* only had one instance of significant differences, both for canine widths. However, since it was not accompanied by canine length it is difficult to draw implications for such a difference.

In a study on *N. vison's* sexual dimorphism, M. Thom argues that ecological niche separation is likely not the driving force behind dimorphism, but simply a mechanism for maintaining the trait (2004). Others yet still argue that relatively short time frames allow for sexual dimorphism to vary and adapt in response to rapid ecological changes, shown by observations of mustelids colonizing a new ecosystem and displaying greater morphological variation best explained by a niche-based hypothesis (Dayan 1994). Some research in the field has attempted to address this discrepancy, but will require very long-term periods of study to strongly infer one way or the other (Powell 1997).

The results of this study may provide more evidence for niche-variable expressions of sexual dimorphism given the deviation from predicted dimorphism from studies conducted elsewhere. It is possibly a later utilization of the ancestral trait used for sexual selection. Although more species should be examined to infer anything about the phylogenetics of this trait, it will be especially interesting to track the further variation of dimorphism in Minnesota as ecological resources change over time.

Bibliography

Meiri, S., T. Dayan, and D. Simberloff. 2005. Variability and correlations in carnivore crania and dentition. Funct. Ecol. 19:337–343.

Zschille, J., N. Stier, and M. Roth. 2009. Gender differences in activity patterns of American mink *Neovison vison* in Germany. European Journal of Wildlife Research. 56:187-194.

García, P. 2010. Female multiple copulation in the invasive American mink (Neovison vison). North. West. J. Zool. 6:138–139.

Johnson, A. 1970. Biology of the raccoon (*Procyon lotor* varius Nelson and Goldman) in Alabama. Agric. Exp. Stat. 402:1-148.

Fritzell, E. 1978. Aspects of raccoon (*Procyon lotor)* social organization. Can. Jrn. Zoology. 56:260-271.

Gittleman, J. L., and B. V. a N. Valkenburgh. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size , phylogeny , and behavioural ecology. J. Zool. 242:97–117.

Koepfli, K.-P., K. a Deere, G. J. Slater, C. Begg, K. Begg, L. Grassman, M. Lucherini, G. Veron, and R. K. Wayne. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol. 6:10.

Shine, R. 2010. Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence. Qrt. Rev. Bio. 64:419–461.

Moors, P. J. 2007. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. Oikos. 34:147–158.

Thom, M. D., L. a. Harrington, and D. W. Macdonald. 2004. Why are American mink sexually dimorphic? A role for niche separation. Oikos 105:525–535.

Meiri, S., T. Dayan, and D. Simberloff. 2005. Variability and correlations in carnivore crania and dentition. Funct. Ecol. 19:337–343.

Powell, R. a, and C. M. King. 1997. Variation in body size, sexual dimorphism and age-specific survival in stoats, Mustela erminea (Mammalia: Carnivora), with fluctuating food supplies. Biol. J. Linn. Soc. 62:165–194.

King, C. 1989. The advantages and disadvantages of small size to weasels, *Mustela* species. Carnivore Behavior, Ecology, and Evolution. 2:302-334.