Factors that describe and determine the territories of canids

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A home range is distinguished as the area of a landscape that an individual or pack resides in. A territory is made distinguishable from a home range because the resident(s) actively defend their territory from others. There has been a considerable amount of experimental and theoretical research done in concern to territories of members of the family Canidae. Many papers have attempted either model territories or experimentally analyze the landscape or ecological factors that determine canid territories.

Lewis and Murray (1993) first analyzed how to model wolf territories by using partial differential equations. They formed an equation based on scent markings in the form of raised leg urination (RLUs) and simple diffusion to describe wolf movement. They also created an equation to describe the distribution of RLUs. Using these two equations, Lewis and Murray (1993) were able to successfully model territoriality in wolves by accurately predicting higher presence of RLUs at territory edges, and the presence of buffers between wolf territories. White et al. (1996) expanded upon the model of Lewis of Murray (1993) by analyzing seasonality of wolf territories. They use partial differential equations to represent the importance of dens in the summer. I feel that this was an important direction to take in the theory of modeling territories because the den becomes a focal point during the breeding season, and this is shown by White et al. (1996) in the fact that the den is located at the center of modeled territories. However, when this focal point is not present for extended periods of time, territories will eventually breakdown (White et al. 1996). This does not seem like a realistic expectation. One of the key factors defining a territory is that the residents actively defend it. To me, stating that territories breakdown also insinuates that wolves are no longer defending their localities from conspecifics, which is very unrealistic. This result points out a major flaw in Lewis and Murray (1993), White et al (1996) and many other theoretical modeling researches. This is that they do not test their models against real world data. Mooncraft et al (2006) do take this important step and test the model from Lewis and Murray (1993) with data on a coyote population.

It is slightly unrealistic to expect that scent markings are the sole determinant in home range size and shape. In fact, it was determined that the model from Lewis and Murray (1993) was inadequate in describing the territories of coyotes, and that to form an adequate model, prey abundance had to be incorporated (Moorcraft et al. 2006). I feel that this shows the importance of landscape and ecological factors in determining territory size and shape. It is unrealistic to expect that canids determine their territory simply by occupying habitat in which no conspecifics are present. It was determined that models incorporating RLUs and prey abundance most accurately determined coyote territories.

Moorcraft et al. (2006) shows the importance of examining the landscape and ecological factors that determine affect territories. Atwood (2006) found that group size and territory size of coyotes are determined independently by landscape features. I found this interesting because prior to my readings, I had assumed that group size and territory size were directly correlated. Instead, territory size was determined by distance between patches of forest, while group size was determined by forest area (Atwood 2006). Another factor that is surprisingly correlated with increasing territory size is increasing latitude, and this relationship is independently of any landscape or ecological factor (Jedrzejewski et al. 2007). Unfortunately, they did not address morphological differences in wolves at different latitudes, which could affect resource demands.

Several canids, especially coyotes, have become very adapted to the human presence and have learned how to live along humans, and several papers have analyzed how human disturbances affected coyote territories. The presence of a landfill in Mexico drastically affected the size of coyote home ranges. A landfill provides a continuous source of highly abundant resources, and this causes coyotes to reduce the total area of territories compared to coyotes in a nearby forest (Hidalgo-Mihart et al. 2004). This is likely because coyotes do not need large territories for to find adequate resources. In this sense, it can be said that a landscape feature created by humans has a positive effect coyotes. It has also been shown that coyotes are capable of perceiving human presence, and decrease home range as density of human development increases (Atwood et al. 2004). Atwood et al. (2004) state that coyote territories decrease in size in an attempt to avoid contact with humans. This would mean that human presence is having a negative impact on coyotes, as they are limited in dispersal and density by human presence. When you take into account the contrasting effects of humans on coyotes in Atwood et al (2004) and Hidalgo-Mihart (2004), it is that humans have mixed effects on coyote territories.

An interesting perspective taken by Jedrzejewski et al. (2008) was to examine how range use differed among individuals within the same pack. It was found that breeding wolves utilized more of the territory than non-breeding wolves, though Jedrzejewski et al. (2008) does not offer any possibly hypothesis for why this might be. It is possible that it is the result of social behavior and the existence of a hierarchy. Also, breeding individuals may be larger, increasing their need for resources. I feel that the analysis of individual territory use within a pack deserves more attention in future studies. It also gives light to importance of the individual when analyzing territories in canids.

The importance of the individual is strengthened when considering canids that do not form packs. Some large canids, such as the maned wolf, do not form packs (Jacamo et al. 2009). One interesting aspect of territories held by these solitary wolves is that there is significantly more overlap with members of the opposite sex, as opposed to members of the same sex (Jacamo et al. 2009). Additionally, individuals of the same sex had virtually no overlap in core area, the area of the territory that receives the most use, while individuals of the opposite sex did (Jacamo et al. 2009). This is distinct from the canids that form packs, which have similar territory overlaps with individuals regardless of sex (Jedrzejewski et al. 2007, Young et al. 2008), and I feel that it is very important to create models for predicting territories of solitary and social canids seperately. The kit fox is another canid that does not form packs. They are subjected to intense interference competition from coyotes (List and Macdonald 2003). This threat of mortality causes kit foxes to shift their territories from desirable prairie dog village habitat (List and Macdonald 2003). This paper shows that when considering territory formation, one cannot consider only conspecifics. Instead, all potential competitors must be considered ,which I feel is very important.

The consideration of sympatric species is used by Roth et al. (2008) to model how the presence of coyotes may affect the establishment of a reintroduced population of red wolves. As expected, competition from coyotes would decrease the population size of red wolves; however, I did not expect to see that the size of red wolf territories would increase in the presence of coyotes (Roth et al. 2008). It is generally accepted that territory size will increase with decreasing population density. However, in spite of the fact that coyote presence drives down red wolf population, it actually increases the overall canid population. I had expected this increase in canid density to decrease red wolf population density. I feel that this is prime example of when models need to be tested against real data. However, due to the red wolf's status as an endangered species, it would be difficult if not impossible to form an experiment on this.

Recently, scientists have started to focus on performing long term studies on territories, allowing insight into their stability. I feel that this a more insightful approach than short term studies because variables such as prey abundance that affect territories (Atwood 2004) change over time. Kitchen et al. (2000) showed that there was significant overlap in territories that were monitored 10 years apart from each other, and hypothesize that coyotes inherit territories. Young et al. (2008) found that temporary increases in food abundance (in the form of supplemental feeding stations) at the edges of territories did not shift core area away from the den during the breeding season. Young et al. (2008) also found that surviving resident coyotes did not shift territories to incorporate supplemental feeding stations after intensive removal of conspecifics. Instead, transient coyotes would immigrate into the study area and take over vacated territories (Young et al. 2008). The results of Young et al (2008) and Kitchen et al. (2000) indicate that coyote territories are very stable over time, and that short-term disturbances are unlikely to alter territories, especially during the breeding season.

Canid territories are a very complex. It is worthwhile to attempt to form mathematical models that describe and predict territory size and shape, but these models need to be tested against experimental and field data to confirm their accuracy. It is also important to consider how human presence affects canid territories, as some species may be able to exploit this. Additionally, not all canids exhibit the same behaviors, as some form packs and some are solitary. This distinction is important because it does alter territory formation. Competitors must also be considered when analyzing territories, as canids that are not top predators may establish territories where they can superior competitors. In spite of all these complexities, or perhaps because of them, it has been observed that some canids have very stable, multigenerational territories. These observations show that analysis of canid territories should begin to focus on long term studies, as canid territories may change from season to season or year to year as long term disturbances are introduced.

Annotated Bib

Atwood, Todd C. 2006. The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. Canadian Journal of Zoology 84: 80-87.

The author used the landscape metrics of forest area, corridor area, and nearest-neighbor forest area to fit models predicting group size and territory size for coyotes. It was found that distance between patches and corridor area determined territory size, while forest area was positively related to group size and corridor area was negatively associated with group size. These findings show that there may not be a relation between territory size and group size in coyotes. Instead, territory size increases as resources become more aggregated and group size increases as the abundance of continuous food and cover resources (forests) increases. I was surprised to find this out, as I thought group size and territory size were directly correlated. However, they make sound arguments and I agree with there findings.

Atwood, Todd C, Harmon P. Weeks, and Thomas M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 68:1000-1009.

This paper focuses on how levels of human development affect the size of coyote home ranges and diel activity patterns, and to determine how much coyotes exploit spatial elements in the landscape. It was found that increased densities of human development decreases the area of coyote home ranges, daily movement, and hourly rate of movement. This is in spite of the result that all home range core areas were predominantly forest. This leads to suggestion that coyotes are capable of perceiving human presence and attempt to avoid humans as much as possible. The avoidance of humans is likely to lead to a contraction in home range size, which was observed in the data. This implies a negative effect of human presence on coyotes, which is contrary to Hildago-Mihart et al (2004) (see below0.

Hidalgo-Mihart, Mircea G., Lisette cantu-salazar, Calos A. Lopez-Gonzalez, Erin C. Fernandez., and Alberto Gonzalez-Romero. 2004. Effect of a landfill on the home range and group size of coyotes (*Canis latrans*) in a tropical deciduous forest. Journal of Zoology 263:55-63.

The size of seasonality of home ranges for coyotes in two different habitats, landfill and tropical deciduous forest, were compared. The authors found that coyotes that lived in the landfill had much smaller home ranges, and attributed this to a constant large supply of food. I found this paper particularly interesting because it shows anthropogenic effects on home ranges. The landfill provides a unique habitat for coyotes and those who live inside of it are able to scavenge of its constant supply of food. This reduces the need for the coyotes to increase home ranges in order to find more resources, and therefore can be said to have a positive effect on the coyotes. I feel that this is a sound assumption, as coyotes are extraordinary in their adaptive abilities and are capable of exploiting habitats altered by humans.

Jacomo, Anah Tereza De Almeida, Cyntia Kayo Kashivakura, Claudia Ferro, Mariana Malzoni Furtado, Samuel Perez Astete, Natalia Mundim Torres, Rahel Sollmann, and Leandro Silveira. 2009. Home range and spatial organization of maned wolves in the Brazilian grasslands. Journal of Mammalogy 90:150-157.

The authors attempt to estimate home range size and overlap of individual maned wolves. The interesting aspect of this paper is that maned wolves are mainly solitary, as opposed to other large canids that form packs. They showed that the peripheries of the wolves' home range overlap. However, individuals of the same sex show very little overlap in the core area of the home range, while the core area of home ranges for individuals of the opposite sex had more overlap. This finding interests me in that it shows that individuals are less territorial to members of the opposite sex, showing that territoriality is not based simply on resource needs, but also on mating. This result is also very different than what would be expected from canids that form packs. Of all the papers I read, this one had the most interesting results.

Jedrzejewski, Wlodximierez, Kryzsztof Schmidt, Jorn Theuerkauf, Bogumila Jedrzejewski and Rafal Kowalcyk. 2007. Territory size of wolves *Canis lupus*: linking local (Bialoweiza Primeval Forest, Poland) and holarctic-scale patterns. Ecography 30:66-76.

The authors analyze several characteristics of wolf territories. First, they analyze if all pack members utilize the same range of the territory, finding that non-breeding individuals use smaller ranges than breeding individuals. They also performed a literature in order to fit a model that would predict territory size, finding that latitude is positively correlated with territory size and prey abundance is negatively correlated with territory size. This is the only paper I read that analyzed differences in range between members of the same pack and their results are intriguing, as dominant members of the pack utilize more of the home range than subordinate individuals. Unfortunately, the authors do not expand upon this result in their discussion, though I feel this is simply the result of a social hierarchy in the pack. They do expand upon the idea that latitude is the main determinant on territory size, and that this effect is independent of prey abundance. This latitudinal effect could instead be the result of increased body size of wolves at higher latitudes, and, as a result, increased demand for prey.

Kitchen, Ann M., Eric M. Gese, Edward R. Schauster. 2000. Long-term stability of coyote (*Canis latrans*) home ranges in southeastern Colorado. Canadian Journal of Zoology 78:458-464.

Coyotes were monitored using radiotelemetry during two periods of time about eight years apart in order to determine the consistency of home ranges. Substantial overlap of home ranges was found between the two periods, exhibiting that coyote packs maintain stable home ranges. What I find particularly interesting about this is that the beginning of the first period and the end of the second period were 14 years apart. This is greater than the lifespan of coyotes, and could show the pack territories have a longer duration than the individuals that make up the pack, with offspring inheriting home ranges from their parents. An alternative explanation not mentioned by the authors is that a new pack simply takes the place of an old pack after that pack has disbanded. Another interesting point in this article is that home range decreased in the second observational period when prey density was higher. This implies a relationship between home range dynamics and foraging ecology.

Lewis, M. A. and J.D. Murray. 1993. Modeling territoriality and wolf-deer interactions. Nature 366: 738-740.

The authors of this paper attempt to model territorial patterns of the grey wolf under the assumptions that wolf movement is in the form of simple diffusion and is mediated by the presence or absence of scent markings in the form of raised leg urination (RLUs). I found it interesting that a simple model based on scent markings a diffusive movement, and without considering any landscape or ecological variables, was able to create a model with defined territories and buffer zones between those territories. I also liked that their model predicted that RLUs would be in the greatest density at the boundaries of the territory. I would like to see if this model would accurately predict territory size if pack size was incorporated into the model. They also use partial differential equations to predict that deer will be in high abundance in buffer zones, but that is outside the scope of my interest in this paper.

List, Rurik and David W. Macdonald. 2003. Home range and habitat use of the kit fox (*Vulpes macrotis*) in a prairie dog (*Cynomys ludovicianus*) complex. Journal of Zoology 259:1-5.

In this paper, the authors attempt to describe the home range size and determine habitat use by red foxes. They find that red foxes at their study site have similar home range sizes to other red fox populations, but that red foxes do not use prairie dog villages as much as would be expected. The reason I chose to read this paper is that unlike wolves and coyotes, red foxes are not considered to be top predators, and face intense interference competition from other canids such as coyotes. The authors feel that this is evident in the habitat use of red foxes. Red foxes did not establish home ranges in and around the prairie dog complex as much as would be expected. However, coyotes did establish home ranges at those locations. It is likely that red foxes establish their home ranges elsewhere to reduce mortality. This paper shows further evidence that one must consider more than just conspecifics when determining the location of home ranges.

Moorcraft, Paul R., Mark A. Lewis, and Robert L. Crabtree. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. Proceedings of the Royal Society of Biology 273: 1651-1659.

The model proposed by Lewis and Murray (1993) (see above) was tested on coyotes and found to be a poor fit to actual territories. The authors proposed landscape features and prey abundance as potential reasons for the poor fit, and tested models incorporating these factors with scent marks. They found that a model incorporating scent marks and prey abundance provided the best fit to the actual territories The fact that incorporating one extra parameter into a predictive model can drastically improve its fit (ΔAIC=2597) shows that territories are very complex and dependent on many factors. They show that coyotes do not simply determine territories by living where their conspecifics do not.

Roth, James D., Dennis L. Murray, Todd D. Steury. 2008. Spatial Dynamics of sympatric canids: Modeling the impact of coyotes on red wolf recovery. Ecological Modeling 214:391-402.

The authors apply space-use models for coyotes and red wolves at the pack level to determine the effect coyote on the success of red wolf reintroductions. The authors made 2 assumptions in their model that I found intriguing. They assumed that territories could overlap. However, they did not allow overlap of a “core area” located in the center of the territory. The core area is that in which the pack spends the most time. This is intriguing because the authors are working with very limited field data, and they are making assumptions about space-use and frequency of interactions. The most interesting result of this paper is that while red wolf population decreased in the population density when coyotes entered the model, the average home range size increased. While this follows observations of home range size decreasing for a species as its population density decreases, the overall canid population is actually higher. A possible reason for this result is that coyote home ranges are much smaller than red wolf home ranges.

White, K. A. J., M. A. Lewis, and J.D. Murray. 1996. A model for wolf-pack territory formation and maintenance. Journal of Theoretical Biology 178: 29-43.

With the help of White, Lewis and Murray expand the analysis their model proposed in 1993 (see above). In this paper they show that wolf packs will form symmetrical home ranges around dens in the absence of competition from conspecifics. This shows the importance of dens in determining territory. Once other packs are introduced, territories become asymmetrical as a result of competition for space and avoidance of territorial markings. Seasonal differences in territories were also examined because wolves no longer focus activities around a den during winter. It was found that if this condition would last for long periods, territories would begin to breakdown. This interests me because the concept of a territory is that it is a home range that is actively defended. Proposing that territories will break down may infer that wolves will alter their behavior, as they no longer actively defend themselves from conspecifics.

Young, Julie K. Selma N. Glasscock, and John A. Shivik. 2008. Does spatial structure persist despite resource and population changes? Effects of experimental manipulations on coyotes. Journal of Mammalogy 89: 1094-1104.

The authors aim to determine if changes in the spatial distribution of food affect by using supplemental feeding stations. They found that coyotes did not alter the location of the core area of their territory to include feeding stations, although there was evidence of frequent use of feeding stations. The other aim of the study was to find if spatial distribution would change after intensive removal, and no effects were found. One reason that core areas likely did not change is that the experiment occurred during pup-rearing season, when coyote core areas are determined by den location. This shows that while prey abundance can affect the size and distribution of territories, as seen in other studies, there are other overriding factors that are more important for determining the spatial distribution of coyotes. This shows that determining territory location and size are complex, as they are affected by many factors, and the importance of these factors may change from season to season. One fault with this paper is that it fails to look at shifts in long term prey abundance. It is possible that coyotes may change the location of den sites to be closer to supplemental feeding sites if those sites persist throughout the year.