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Differences between northern and southern female coyotes

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ABSTRACT.—The coyote (*Canis latrans*) has a wide distribution range, spanning boreal forests from the north of the continent to tropical environments in Central America, showing great adaptation and plasticity. Bergmann's rule states that individuals inhabiting colder climates are larger than those in warmer climates. It is suggested that in carnivore species, litter size is influenced by allometric constraints such as maternal body size. The aim of this study is to analyze the relations using correlation between female coyote mass, latitude, and litter size. Using data compiled from the literature, I carried out statistical analyses to correlate female body size, litter size, and latitude for coyotes across their distribution range. The results indicated a soft significant correlation between female body size and latitude, confirming Bergmann's rule. However, no significant correlation was found between litter size and latitude or between litter size and female body size; litter size in coyotes remains roughly uniform across their distribution range.

RESUMEN.—El coyote (*Canis latrans*) tiene un amplio rango de distribución, que abarca desde bosques boreales en el norte del continente hasta ambientes tropicales en Centroamérica, mostrando una gran adaptación y plasticidad. La regla de Bergmann establece que los individuos en climas más fríos son más grandes que los que habitan en los climas más cálidos. Se sugiere que en las especies el tamaño de la camada está influenciada por restricciones alométricas como el tamaño del cuerpo materno. El objetivo de este estudio es analizar la relación entre el peso de las hembras de coyote, la latitud y el tamaño de la camada. Utilizando datos recopilados de la literatura, llevé a cabo análisis estadísticos para correlacionar el tamaño del cuerpo de la hembra de coyote con el tamaño de la camada y la latitud en su rango de distribución. Los resultados indicaron una correlación ligeramente significativa entre el tamaño del cuerpo de las hembras y la latitud, lo que confirma la regla de Bergmann. Sin embargo, no se encontró una correlación significativa entre el tamaño de la camada y la latitud o el tamaño de la camada y el tamaño del cuerpo de las hembras. Ya que, se encontró que el tamaño de la camada en los coyotes es similar a lo largo de todo su rango de distribución.

The distribution range of a species is related to climate as well as geographic position (latitude, longitude, and elevation; Townsend Peterson et al. 2011). The species that are widespread stand out due to their adaptations to different environments and the relative ease with which they can colonize new ones. One of these adaptations is shown by a correlation between body size and temperature, a relationship known as Bergmann's rule. The relationship has been documented in multiple mammal species, with individuals from arctic and temperate regions (higher latitudes) being larger than those from equatorial regions (Bergmann 1847, Meiri and Dayan 2003, Blackburn and Hawkins 2004, Rodríguez et al. 2008).

The coyote (*Canis latrans*) is an ideal case study to test these correlations because of its

continuous distribution from Alaska through Central America (Bekoff 1977, Hidalgo-Mihart et al. 2004). The expansion of the coyote's range at the north and east in North America has been associated with body size (Thurber and Peterson 1991). Nowadays, its range is advancing southward; if the coyote reaches northern South America, there are possible routes that could facilitate a rapid spread through the entire continent (Hody et al. 2019, Monroy-Vilchis et al. 2020). This wide distribution reflects the coyote's high genetic plasticity and ability to occupy various habitats, and it is associated with land use and vegetation cover changes (Gompper 2002). Female coyotes have 8 mammary glands (Hildebrand 1952), which represents the theoretical maximum number of pups per litter that could be adequately fed (Stockley and Parker

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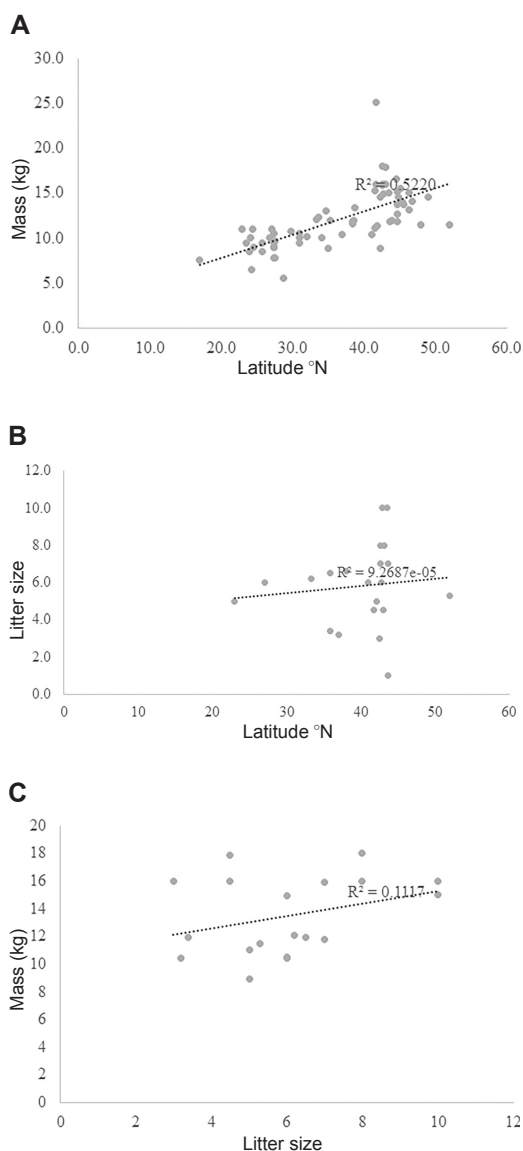


Fig. 1. Graphics for linear regression models. **A**, Female coyote body mass (kg) versus latitude (°N). **B**, Litter size (number of pups) versus latitude (°N). **C**, Female coyote body mass (kg) versus litter size (number of pups).

2002). Females are monoestrous, and the timing of their reproductive cycle varies across the distribution range, with no specific breeding season (Hamlett 1938, Bekoff 1977). Studying coyotes can help our understanding of the relationship between latitude, maternal size, and litter size, since data on carnivore species suggest that reproductive characteristics, such as litter size, are bounded by allometric

constraints (e.g., maternal body size). The aim of this study is to analyze the correlation between female coyote mass, latitude, and litter size. The hypotheses I tested are as follows: (1) female coyotes from higher latitudes are larger in mass than those from lower latitudes; (2) heavier female coyotes have larger litter sizes; and (3) female coyotes from higher latitudes have larger litter sizes.

I compiled data on the average mass of wild female coyotes and litter size across their range through a comprehensive search of literature, the Global Biodiversity Information Facility database (GBIF 2020), and the Mammal Collection from the Centro de Investigaciones Biológicas del Noroeste, S.C. (CIBNOR). Because the usable records were limited in number, I did not restrict the data set to a specific time frame. Additionally, for each record, location was georeferenced in Google Earth Pro (<https://www.google.com/intl/es-419/earth/>).

To test the correlations, I used Pearson's correlation coefficient that is a coefficient of determination (R^2) with simple linear regression (Amat 2016) in the program R (R Development Core Team 2021). I examined all paired combinations of the 3 variables (female body mass, litter size, and latitude), using a significance level of $\alpha = 0.05$.

The results showed a soft (not strong) significant correlation between female body size and latitude ($r = 0.7225$, $t = 8.6178$, $P < 1.658 \times 10^{-12}$, $R^2 = 0.5220$), with the largest females occurring in higher latitudes and the smaller ones in lower regions, supporting Bergmann's rule and confirming the first hypothesis (Fig. 1A, Table 1). However, litter size was not correlated with latitude ($r = 0.0096$, $t = 0.0419$, $P < 0.967$, $R^2 = 9.2687 \times 10^{-5}$; Fig. 1B, Table 2); the most variation in litter size was observed between latitudes of 40 and 50 °N. Female body size was also not correlated with litter size ($r = 0.3343$, $t = 1.4627$, $P < 0.1618$, $R^2 = 0.1117$; Fig. 1C). The range-wide average litter size recorded so far is 5.7 pups (range 1–9; Hamlett 1938). Canids are known to have heavy litters relative to the mother's body mass (approximately 14.4% of the mother's mass; Oftedal and Gittleman 1989). In 90.5% of cases, litter size was smaller or equal to 8 (the number of mammary glands in female coyotes), but in 9.5% of the cases litter size was larger than 8. In these cases, perhaps the mortality index in the pups is higher because the

TABLE 1. Latitude and average mass of female coyotes (*Canis latrans*) across the species' North American range.

Latitude (°N)	Mass (kg)	Locality	Reference
52.0	11.5	Jasper National Park, Alberta, Canada	Bowen 1982
49.0	14.5	Ontario, Canada	Kolenosky 1971
48.0	11.5	N Minnesota, USA	Berg and Chesness 1978
46.8	14.1	SE Québec, Canada	Poullé et al. 1995
46.3	13.1	E New Brunswick, Canada	Dumond and Villard 2000
46.3	15.0	Prince Edward Island, Canada	Parker 1995
45.5	13.7	Somerset, Maine, USA	Richens and Hugie 1974
45.4	14.0	United Counties of Leeds and Grenville, Ontario, Canada	Garvey and Patterson 2014
45.2	15.5	Calais, Maine, USA	Harrison 1986
44.9	14.5	Orono, Maine, USA	Hilton 1976
44.8	11.8	Yellowstone National Park, Wyoming, USA	Crabtree and Sheldon 1999
44.7	15.2	Nova Scotia, Canada	Moore and Millar 1986
44.7	12.6	Nova Scotia, Canada	Sabean 1993
44.7	13.7	Nova Scotia, Canada	Parker 1995
44.5	16.6	Champlain Valley Region, Vermont, USA	Person 1988
44.0	11.9	Adirondacks, New York, USA	Brundige 1993
43.66	11.8	Boylston, New York, USA	GBIF 2020
43.53	15.0	Redfield, New York, USA	GBIF 2020
43.12	16.0	Cato Township, New York, USA	GBIF 2020
43.0	17.9	New Hampshire, USA	Silver and Silver 1969
42.91	16.0	Lafayette, New York, USA	GBIF 2020
42.72	15.0	Sempronius, New York, USA	GBIF 2020
42.65	18.1	Homer, New York, USA	GBIF 2020
42.65	15.9	Homer, New York, USA	GBIF 2020
42.57	16.0	Cortlandville, New York, USA	GBIF 2020
42.4	14.5	West Massachusetts, USA	Lorenz 1978
42.3	8.9	Idaho, USA	Barnum et al. 1979
41.9	11.4	Iowa, USA	Andrews and Boggess 1978
41.7	16.0	Barnstable, Cape Cod, Massachusetts, USA	Way 2000
41.7	25.1	Barnstable, Cape Cod, Massachusetts, USA	Way and Proietto 2005
41.6	11.1	Kenai, Arkansas, USA	Thurber and Peterson 1991
41.6	15.3	Rhode Island, USA	Brown et al. 1993
41.1	10.4	North Coast, California, USA	Neale et al. 1998
38.7	13.4	West Virginia, USA	Houben and Mason 2004
38.6	11.9	West Virginia, USA	Wykle 1999
38.5	11.6	Kansas, USA	Gipson and Kamler 2002
38.5	11.8	Kansas, USA	Gier 1968
37.0	10.4	California, USA	Hawthorne 1971
35.3	11.9	Oklahoma, USA	Young and Jackson 1951
35.1	8.8	Anderson Mesa, Arizona, USA	Witham 1977
34.8	13.0	Arkansas, USA	Gipson 1978
34.2	10.1	New Mexico, USA	Young and Jackson 1951
33.7	12.3	B.F Grant Wildlife Management Area, Georgia, USA	Gates et al. 2014
33.4	12.1	Cedar Creek Wildlife Management Area, Georgia, USA	Gates et al. 2014
32.0	10.2	Tucson, Arizona, USA	Grinder and Krausman 2001
31.0	9.5	New Mexico, USA	Windberg et al. 1997
31.0	10.5	Texas, USA	Young and Jackson 1951
31.0	10.0	Sierra San Pedro Mártir, Baja California, México	Mammal Museum CIBNOR 2021
29.8	10.7	San Luis Gonzaga, Baja California, México	Mammal Museum CIBNOR 2021
28.7	5.5	Misión San Borja, Baja California, México	Mammal Museum CIBNOR 2021
27.5	7.8	Vizcaíno Biosphere Reserve, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.5	9.7	Vizcaíno Biosphere Reserve, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.4	9.0	Corral de Berrendos, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.4	7.8	Corral de Berrendos, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.4	9.5	Corral de Berrendos, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.4	9.0	Corral de Berrendos, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.4	10.5	Corral de Berrendos, Baja California Sur, México	Mammal Museum CIBNOR 2021

TABLE 1. Continued.

Latitude (°N)	Mass (kg)	Locality	Reference
27.4	9.0	Corral de Berrendos, Baja California Sur, México	Mammal Museum CIBNOR 2021
27.1	11.0	15 km E Bahía Asunción, Baja California Sur, México	Mammal Museum CIBNOR 2021
26.8	10.0	50 km S, 28 km W San Ignacio, Baja California Sur, México	Mammal Museum CIBNOR 2021
25.7	9.5	San Jorge, Baja California Sur, México	Mammal Museum CIBNOR 2021
25.7	8.5	San Jorge, Baja California Sur, México	Mammal Museum CIBNOR 2021
24.7	9.0	Isla Magdalena, Baja California Sur, México	Mammal Museum CIBNOR 2021
24.5	11.0	Isla Magdalena, Baja California Sur, México	Mammal Museum CIBNOR 2021
24.3	6.5	Km 76 carretera Transpeninsular, Baja California Sur, México	Mammal Museum CIBNOR 2021
24.1	10.0	El Comitán, Baja California Sur, México	Mammal Museum CIBNOR 2021
23.9	8.5	San Pedro, Baja California Sur, México	Mammal Museum CIBNOR 2021
23.5	9.5	Santiago, Baja California Sur, México	Mammal Museum CIBNOR 2021
23.0	11.0	La Michilía Biosphere Reserve, Durango, México	Servín 2000
17.0	7.5	Santa Catarina Ixttepeji, Oaxaca, México	Monroy-Gamboa 2007

TABLE 2. Latitude, average litter size per female coyote, and season when data were collected across the species' North American range. N/D = no data.

Latitude (°N)	Litter size	Season	Locality	Reference
52.00	5.3	N/D	Alberta, Canada	Nellis and Keith 1976
43.66	7.0	Winter	Boylston, New York, USA	GBIF 2020
43.66	1.0	Winter	Boylston, New York, USA	GBIF 2020
43.53	10.0	Winter	Redfield, New York, USA	GBIF 2020
43.12	8.0	Winter	Cato Township, New York, USA	GBIF 2020
43.00	4.5	N/D	National Elk Refuge, Jackson, Wyoming, USA	Camenzind 1978
42.91	10.0	Autumn	Lafayette, New York, USA	GBIF 2020
42.72	6.0	Autumn	Sempronius, New York, USA	GBIF 2020
42.65	8.0	Winter	Homer, New York, USA	GBIF 2020
42.65	7.0	Winter	Homer, New York, USA	GBIF 2020
42.57	3.0	Spring	Cortlandville, New York, USA	GBIF 2020
42.10	5.0	Spring	Greater Chicago Metropolitan Area, Illinois, USA	Hennessy et al. 2012
41.70	4.5	Spring	Barnstable Cape Cod, Massachusetts, USA	Way et al. 2001
38.03	6.6	Spring	Sierra Nevada, California, USA	Sacks 2005
41.00	6.0	N/D	Iowa, USA	Andrews and Boggess 1978
37.00	3.2	N/D	SE Colorado, USA	Gese et al. 1989
35.90	3.4	N/D	Gibson and Carroll Counties, Tennessee, USA	Stephenson and Kennedy 1993
35.90	6.5	N/D	Tennessee, USA	Kennedy et al. 1990
33.30	6.2	N/D	Barnwell, Allendale, South Carolina, USA	Kilgo et al. 2017
27.00	6.0	N/D	Webb County, Texas, USA	Knowlton et al. 1999
23.00	5.0	Summer	La Michilía Biosphere Reserve, Durango, México	Servín 2000

pups do not obtain enough maternal milk. The findings of Asdell (1964), that an average of 6.23 embryos were produced across a sample of 1370 cases, strengthen the previous statement.

Hypotheses 2 and 3 were rejected at this geographic scale. No significant correlation was found between litter size and female body size

or between litter size and latitude, although smaller females apparently had smaller litter sizes. There is a high possibility that significant correlations might emerge with the incorporation of more data.

The great genetic plasticity that allows coyotes to occur in a wide variety of habitats and

climates does not seem to affect reproductive aspects. Litter size data from the same latitude were recorded at different seasons of the year, which implies seasonally different available food and prey (Table 2). Thus, variations in litter size might rather be related to food availability in different environments (Gier 1975, Gompper 2002). Potential prey and carrion that coyotes feed on in temperate regions are (or come from) larger animals than found in the tropics (Bekoff and Wells 1980). The results of the present study indicated that there is not a significant correlation of latitude with litter size, so my results imply that having larger available prey does not translate into more pups. Breeding female coyotes need about 900 g of additional food per day, compared to nonbreeding females (Gier 1975). Another important variable is that the predator control programs in the USA showed little success, because in the long term, coyote populations increased instead of decreased; the response of female coyotes to predator control was to produce larger litter sizes (Knowlton 1972, Gompper 2002). So, there are exogenous factors (e.g., predator control programs, land use and vegetation cover change, quality and availability of food and prey) and endogenous factors (e.g., genetic information, hybridization) that influence litter size in coyotes apart from the environment (climate) and the mother's size (McNab 1989, Thurber and Peterson 1991).

In terms of ecosystem conservation and management, the litter size of coyotes does not vary significantly across their distribution range or with female body size.

Because coyotes are expanding their distribution range, adequate strategies should be promoted to improve ecological monitoring of coyote colonization in South America in order to describe the changes that occur in those animal communities and ecosystems. This monitoring would provide important information that, at present, is poorly known.

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