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ORIGINAL ARTICLE

Biogeographical patterns in the Western Palearctic: the fasting-endurance hypothesis and the status of Murphy's rule

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ABSTRACT

Aim In Europe, winter severity is positively correlated with longitude. We test how this climatic cline affects biogeographical patterns in Western Palearctic homeotherms.

Location Eurasia, west of 60° longitude.

Methods We test the effects of longitude on body size of carnivores, using cranial measurements of 2002 specimens belonging to 11 species. We test the effects of longitude on migration patterns of birds by comparing which populations of partial migrants are sedentary and which undergo winter migration.

Results Carnivore body size does not vary consistently with longitude. Populations of partial migrants are more likely to be sedentary in western Europe and to migrate from eastern Europe than vice versa.

Main conclusions Longitudinal patterns in climate exert a selective force on birds but do not affect carnivore size in a consistent, predictable manner. We find no support for the mechanism suggested to promote size change, namely the fasting-endurance hypothesis.

Keywords

Bird migration, body size, Eurasia, fasting endurance, geographical variation, latitude, longitude, seasonality.

INTRODUCTION

Climate has a profound effect on various biogeographical patterns in organisms, with temperature often considered a major factor (Wallace, 1876; Brown & Lomolino, 1998). Latitude is highly correlated with temperature and with many other climatic variables. It is therefore latitude that receives most attention when biogeographical patterns related to climate are analysed. It is not uncommon, however, for factors other than latitude to play an important role in shaping biogeographical patterns (Hawkins & Diniz-Filho, 2004). The variance and predictability of climatic conditions may be as significant as mean temperatures in producing biogeographical patterns (Yom-Tov & Nix, 1986). These factors are not necessarily correlated with latitude. Here we examine the effects of longitude, correlated with the degree of seasonality, on biogeographical patterns in the Western Palearctic.

Body size of animal populations often varies greatly in relation to environmental conditions. Homeotherm body size generally varies in accord with the empirical generalization known as Bergmann's rule (Bergmann, 1847; Mayr, 1963; Blackburn *et al.*, 1999; Meiri & Dayan, 2003), i.e. bigger individuals within a species are found at higher latitudes (Rensch, 1938; Mayr, 1942, 1956). Latitude itself, however, does not influence body size, so the correlation between latitude and size reflects selective forces that covary with latitude. Many such variables have been suggested, the most obvious of which is temperature (Bergmann, 1847). Other variables that covary with latitude and are thought to influence body size include primary productivity (Rosenzweig, 1968; Geist, 1987), wet bulb temperatures (James 1970), interspecific competition (McNab, 1971) and night length (Kolb, 1978).

A compelling mechanism, suggested by Lindsey (1966) for poikilotherm vertebrates and formulated by Calder (1974, 1984) for birds and by Boyce (1978, 1979) for mammals,

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involves fasting endurance. Fasting endurance increases with mass (Morrison, 1960; Calder, 1974, 1984), so in unpredictable environments animals may benefit from growing large (Calder, 1974; Boyce, 1978) despite the extra cost of maintaining a larger body (McNab, 1971, 1999, see also Dunbrack & Ramsay, 1993). In predictable, but food-limited environments, however, it is smaller individuals that have an advantage (Millar & Hickling, 1990). Boyce (1978) explained geographical variation in the body size of muskrats [*Ondatra zibethicus* (L.)] in terms of the seasonality of the environment. He interpreted his results as supporting a hypothesis that animals in seasonal environments are more likely to endure food shortages and that larger size therefore confers a selective advantage in such environments. Lindstedt & Boyce (1985) argued that 'fasting-endurance allometry contributes to Bergmann's rule, since cooler climates tend also to be more seasonal and are thus more likely to impose a fasting-endurance crisis' (1985, p. 876).

Murphy (1985) used the seasonality hypothesis to explain geographical variation in body size of house sparrows [*Passer domesticus* (L.)]. House sparrows conform to Bergmann's rule in North America but not in South America, New Zealand, or in their native European range (Johnston & Selander, 1973; Baker, 1980; Murphy, 1985; Yom-Tov, 2001). Murphy (1985) explained this pattern as due to differing geography of climatic conditions in Europe and North America: in Europe winter severity is positively correlated with longitude, rather than with latitude. He found sparrow size in both continents (and in New Zealand) to be positively correlated with the annual temperature range, i.e. with more seasonal environments (Murphy, 1985), and explained the correlation by the less predictable nature of more seasonal habitats.

A similar pattern to the one described by Murphy (1985) for sparrows is found in the stoat (*Mustela erminea* L.; Ralls & Harvey, 1985; Erlinge, 1987; Meiri *et al.*, 2004a), conforming to Bergmann's rule in North America but not in Europe. However, other carnivores in our analysis (Meiri *et al.*, 2004a) that showed different size clines in North America than in Europe (wolves, *Canis lupus* L., see also Davis, 1981) showed the opposite pattern or an ambiguous one (brown bears, *Ursus arctos* L., Rausch, 1963; Kojola & Laitala, 2001; Meiri *et al.*, 2004a).

Birds, of course, can circumvent the problem of unpredictable resources by migrating to more benign climates (Safriel, 1995). In the Palearctic, this migration is in a southerly direction, but other patterns exist, including westward migration from northern and eastern Europe (Berthold, 1993, p. 58). Therefore, migrating birds are not as likely as sedentary ones to follow Bergmann's rule (Meiri & Dayan, 2003). In the Western Palearctic this may mean that patterns of migration, as well as patterns in body size, may differ between eastern and western locations.

Is there a consistent tendency for Palearctic species to show biogeographical patterns reflecting the more seasonal climate and colder winters of Eastern as compared with Western Europe? Is there, in other words, a phenomenon that might be termed 'Murphy's rule'?

We sought to test for Murphy's rule using data on two phenomena from two taxa: differential migrating habits of birds and longitudinal size variation in carnivores, for which we have assembled a large set of measurements for other purposes (Meiri *et al.*, 2004a,b), thus enabling us to test longitudinal patterns in this group, as a representative of mammals as a whole.

For carnivores, we predict that size will correlate positively with longitude in the Western Palearctic, at least after the effects of latitude are removed. As minimum temperatures parallel longitude and maximum ones parallel latitude (Murphy, 1985), size should correlate positively with longitude (once we control for latitude). This prediction is based on the assumption that annual temperature range is positively correlated with body size (Murphy, 1985, see also Baumgardner & Kennedy, 1993). Such a pattern would support the hypothesis of an inverse relationship between size and seasonality and minimum January temperatures (i.e. Bergmann's rule, Meiri & Dayan, 2003). This will support the fasting-endurance mechanism as an explanation for size variation. It would also provide some support for the model developed by James (1970) associating clinal variation with small size in hot, humid conditions and large size in cool or dry conditions.

For birds, we test a phenomenon that is regarded as common knowledge among ornithologists (Y. Yom-Tov, pers. comm.), to the point that it has received little qualitative treatment (e.g. Harrison, 1982, p. 18) and, to our knowledge, no quantitative description: species with different migratory behaviour in different parts of their ranges are thought to be sedentary in the western parts of their range more often than in eastern parts of the range, where populations are predicted to be more likely to migrate to milder climates by the fall.

METHODS

For analysis of size variation in carnivores, we measured skulls of Western Palearctic mainland carnivores ranging from latitude 30 northwards (excluding North Africa) and from longitude 60.00 E westward in the following collections (in longitudinal order): Natural History Museum, London; Zoology Museum of Cambridge University; Harrison Zoological Museum; Museu de Zoologia, Barcelona; Muséum National d'Histoire Naturelle, Paris; Institut Royal des Sciences Naturelles de Belgique; University of Amsterdam, Zoological Museum; Muséum d'Histoire Naturelle de la Ville de Genève; Museo Civico di Storia Naturale 'Giacomo Doria', Genoa; National Wildlife Institute, Bologna; Zoologische Staatssammlung, München; Zoological Museum University of Copenhagen; Museum für Naturkunde, Humboldt Universität zu Berlin; Staatliche Naturhistorische Sammlungen, Dresden; Tel-Aviv University Zoological Museum; Natural History Collections, the Hebrew University, Jerusalem; National Science Museum, Tokyo; University of Alaska Fairbanks, Museum of Natural History; Museum of Vertebrate Zoology, University of California, Berkeley; University of Kansas

Museum of Natural History; the Field Museum, Chicago; Carnegie Museum of Natural History; Royal Ontario Museum; US National Museum of Natural History, Smithsonian Institution; American Museum of Natural History; Museum of Comparative Zoology, Harvard University; and Museo Nacional de Ciencias Naturales, Madrid.

Measurements were taken with digital calipers to 0.01 mm precision. We chose condylo-basal length (CBL) as a measure of body size. We used only wild adult specimens (in which there is complete suture closure) and recorded sex and location data for each specimen. We used only specimens for which reasonably accurate locality data were available (error of less than 1° of longitude and latitude, although for the vast majority of specimens latitude was known with much greater accuracy than 1°). Because all carnivores in our sample are sexually dimorphic (Meiri *et al.*, unpubl. data), we analysed sexes separately throughout, using only morphospecies for which we had a minimum of 15 specimens. The longitudinal ranges, from which our specimens originated, span from 10 to 54° (Table 1). We sought correlations between longitude and size using both simple product–moment correlation and multiple regression of size on both longitude and latitude, in order to remove the effect of the latter (Smith, 1999), on longitudinal patterns.

We used distribution maps in Mullarney *et al.* (1999) for information on migratory behaviour of birds. We examined only species present all-year round at some localities, while in other localities of the same latitude they breed in summer and migrate in winter. We divided these species into three categories. (1) Species residing in western longitudes and summer breeding in more eastern ones. These were tallied as supporting Murphy's rule. (2) Species residing in easterly longitudes and summer breeding in more western ones. These were tallied as contradicting Murphy's rule. (3) All other cases (resident in central latitudes and summer breeding in both more westerly and easterly longitudes, and resident in both east and west, but summer breeding in central longitudes) showing no uniform longitudinal pattern were also tallied as contradicting Murphy's rule (see Meiri & Dayan, 2003).

We tested whether results generally agree with predictions using a chi-square test for goodness-of-fit to an extrinsic hypothesis of a 1 : 1 ratio (Sokal & Rohlf, 1995).

RESULTS

Carnivores

Summary statistics for associations between size and longitude in 2002 carnivore specimens belonging to 13 species are presented in Table 1. In only three [*Vormela peregusna* (Güldenstädt), *Mustela erminea* L. and *M. nivalis* L. males] of 24 cases is there a significant positive association between size and longitude after the effects of latitude have been removed. In three cases [*Meles meles* (L.) males, and *Vulpes*

Table 1 Associations between size and longitude in Western Palearctic carnivores.

Species	Sex	*n*	Longitude range (°)	Latitude range (°)	β longitude (corrected for latitude)	*P*	β latitude (corrected for longitude)	*P*	*r* longitude	*P*
Canis aureus	Male	22	12	9	−0.03	0.908	−0.11	0.644	−0.01	0.948
Canis lupus	Female	18	44	22	−0.02	0.921	0.78	0.002	−0.50	0.035
Canis lupus	Male	24	53	29	−0.03	0.897	0.66	0.009	−0.51	0.011
Felis silvestris	Female	15	42	20	0.75	0.154	0.92	0.089	−0.03	0.908
Felis silvestris	Male	33	54	22	0.08	0.790	0.44	0.170	−0.28	0.110
Genetta genetta	Male	15	10	10	0.14	0.743	0.23	0.593	0.31	0.260
Lutra lutra	Female	26	42	21	0.61	0.072	0.47	0.161	0.24	0.247
Lutra lutra	Male	31	35	31	−0.01	0.971	−0.09	0.693	0.04	0.812
Martes foina	Female	85	47	22	−0.05	0.710	0.38	0.003	−0.27	0.013
Martes foina	Male	107	40	24	0.10	0.375	0.33	0.003	−0.07	0.443
Martes martes	Female	53	46	17	−0.02	0.887	0.16	0.271	0.03	0.815
Martes martes	Male	64	24	19	−0.11	0.387	0.29	0.023	−0.13	0.317
Meles meles	Female	93	42	28	−0.17	0.053	0.59	0.000	−0.48	0.000
Meles meles	Male	150	46	29	−0.20	0.032	0.51	0.000	−0.59	0.000
Mustela erminea	Female	97	25	19	0.11	0.288	−0.34	0.002	0.00	0.998
Mustela erminea	Male	139	45	26	0.24	0.013	−0.30	0.002	0.08	0.329
Mustela nivalis	Female	149	47	23	0.04	0.647	−0.37	0.000	0.03	0.743
Mustela nivalis	Male	347	50	26	0.17	0.000	−0.57	0.000	0.23	0.000
Mustela putorius	Female	112	33	18	−0.05	0.580	−0.11	0.258	−0.08	0.428
Mustela putorius	Male	188	44	19	0.01	0.851	0.13	0.076	0.05	0.508
Vormela peregusna	Male	15	15	14	0.63	0.009	0.45	0.047	0.57	0.028
Vulpes vulpes	Female	97	54	32	−0.21	0.034	0.53	0.000	−0.56	0.000
Vulpes vulpes	Male	122	52	34	−0.22	0.018	0.55	0.000	−0.62	0.000

β, Partial regression coefficient; *r*, product–moment correlation coefficient. A *P* value of 0.000 is actually $P < 0.0005$.

vulpes (L.), both sexes] there is a significant negative association between size and longitude. When we do not control for latitude, there are nine significant correlations – only two of those (*Mustela nivalis* and *Vormela peregusna* males) are in the direction predicted, the other seven showing a decrease in size with increasing longitude. In nine cases there is a significant positive association between size and latitude after the effects of longitude have been removed, as predicted by Bergmann's rule (Meiri & Dayan, 2003; Meiri *et al.*, 2004a). *Mustela nivalis* and *M. erminea* show the opposite pattern. In both families, with more than one species (Canidae, Mustelidae), some species decrease in size with longitude and others do not. In the Mustelidae, some species increase in size with increasing longitude, but not even in *Mustela* is such a pattern common in all species.

The correlation coefficient describing size change with longitude is negatively correlated with longitudinal range ($n = 23$, $r = -0.564$, $P = 0.005$), but not with the median longitude of the sample ($n = 23$, $r = -0.006$, $P = 0.98$).

Birds

Data on bird species analysed are presented in Appendix 1. Eighty-five species vary in their migratory habits in accord with the prediction, 14 vary in the opposite direction and 28 species show no clear pattern. Thus, the majority of species that breed in the Western Palearctic and vary in relation to wintering in their breeding ranges do so in the direction predicted (chi-square test for goodness-of-fit, $\chi^2 = 14.56$, $P < 0.0005$). The numbers of orders, families and genera in which the majority or the minority of species conform to the expected patterns are given in Table 2. In no bird order where $n > 2$ species do a majority of species vary opposite to the prediction.

In 13 of 24 genera with $n > 1$ bird species, and in eight of 10 genera with $n > 2$ species, some species vary according to prediction and others do not. The corresponding values for families and orders are 15 of 23 and five of seven, respectively. Thus we believe phylogenetic affinity does not affect the tendency to follow the expected pattern.

DISCUSSION

Western Palearctic carnivores do not usually increase in size with longitude. Nor does size tend to decrease with longitude, as might have been suggested by the product–moment correlations alone (see also Chylarecki *et al.*, 1997), as there are similar numbers of cases of significant negative and positive correlations between size and longitude after the effects of latitude are removed. These results suggest either that the fasting-endurance hypothesis is incorrect (Dunbrack & Ramsay, 1993), or that the degree of seasonality cannot be equated with the unpredictability of the environment and thus with the time an animal is likely to endure without feeding. Possibly, carnivores are not as sensitive to variations in primary productivity as are more herbivorous mammals, which rely more directly on primary productivity. However, the dependency of carnivores on fluctuating levels of available prey, especially if eastern rodents tend to have a higher proportion of hibernators, may actually mean that their higher position in the food web should make them more sensitive to such variation. This question obviously merits further research.

Table 2 Numbers of orders, families and genera of Western Palearctic birds in which the majority or the minority of species vary according to predictions

Taxon	Over 50% of species sedentary in the west and migratory in the east	50% or less of species sedentary in the west and migratory in the east
Orders	10	4
Families	27	11
Genera	54	31

Previous research has demonstrated that ecological character displacement can affect size patterns related to climatic gradients (Dayan *et al.*, 1989, 1991). It is possible that selective forces related to competition may override the effect of climatic forces, although the likelihood that they will do so to the extent of entirely hiding actual patterns is low.

Latitude certainly does have a predictable effect on the sizes of many homeotherms, including carnivores (Meiri & Dayan, 2003; Meiri *et al.*, 2004a, this study). However, if, as Murphy (1985) suggested, seasonality in the Western Palearctic correlates with longitude to a larger extent than with latitude, then this variable is probably not the one driving carnivore size clines. We know of no empirical data supporting the hypothesis that annual temperature range is highly correlated with actual periods of food shortage. Seasonality may be exerting a selective force driving evolutionary size change directly through the effects of both minimum and maximum temperatures (see discussion in Meiri & Dayan, 2003).

Western Palearctic birds, on the contrary, show a striking longitudinal pattern in their tendency to migrate, with eastern ones much more likely to do so (Harrison, 1982). We believe this pattern is even stronger than these numbers suggest, as in none of the cases that we classify as opposing the rule is there a very large eastern range of residency and a large western one in which birds spend only the summer. The reverse situation – a large area of residency in the west and a large summer breeding range in the east – is relatively common (see maps in Mullarney *et al.*, 1999). The severe winters in eastern longitudes force bird populations to migrate, whereas the more benign winter climates of westerly longitudes enable birds to stay in their breeding grounds all year, thus avoiding the costs of migration (Cox, 1985; Böhning-Gaese *et al.*, 2000).

Obviously, not all Palearctic birds are summer breeders in parts of their range and permanent residents in others. Some can tolerate more severe climatic regimes and remain in one place year round; others are obligatory migrants, not residing in any one place all year, and other patterns exist.

The pattern qualitatively described for differential migrants is quantitatively confirmed – within a large portion of the migratory avian fauna, more easterly populations are more likely to be migratory than western ones. While the effects of the influences of the climatic pattern on bird size remain to be tested, no pattern is found for carnivore body size. There is no common tendency for size change with longitude in the Western Palearctic, contrary to the predictions of the seasonality and fasting-endurance hypotheses.

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BIOSKETCHES

Shai Meiri is a PhD student studying the evolution of body size of island carnivores. He is interested in the evolution of body size in mammals at both the microevolutionary and macroevolutionary scales. Other fields of interest are the relationship between biogeography and evolution, late Pleistocene mammalian extinctions, and major innovations in vertebrate evolution.

Tamar Dayan is an Associate Professor of Zoology, with a research interest in the evolution of mammals within ecological communities. Her research involves both recent mammals (museum specimens and ecological communities in the field) and fossil and subfossil ones. Previous morphological studies include character displacement and sexual size dimorphism.

Daniel Simberloff is Nancy Gore Hunger Professor of Environmental Studies. He is interested in biogeography, population and community ecology, evolution, and invasion biology – patterns displayed by species introduced outside their geographical ranges, the impacts such species have on the communities they invade, and the means by which such invasions can be managed.

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Appendix 1 Bird species resident in parts of the western Palearctic and summer-breeding in other parts. Bird species sedentary in the east and migratory in the west (Yes), sedentary in the west and migratory in more easterly longitudes (Opposite), and species showing no clear longitudinal pattern

Species	Sedentary in the east and migratory in the west?
Anas clypeata	Yes
Anas crecca	Yes
Anas platyrhynchos	Yes
Anas strepera	Yes
Anser anser	No clear pattern
Aythya ferina	Yes
Aythya fuligula	Yes
Aythya nyroca	No clear pattern
Bucephala clangula	No clear pattern
Cygnus cygnus	Yes
Cygnus olor	Yes
Marmaronetta angustirostris	No clear pattern
Mergus merganser	Yes
Netta rufina	No clear pattern
Oxyura leucocephala	Yes
Somateria mollissima	Yes
Tadorna ferruginea	No clear pattern
Tadorna tadorna	Yes
Burhinus oedicnemus	Yes
Charadrius alexandrinus	No clear pattern
Charadrius hiaticula	Yes

Appendix 1 *continued*

Species	Sedentary in the east and migratory in the west?
Vanellus vanellus	Yes
Haematopus ostralegus	Yes
Larus argentatus	Yes
Larus canus	Yes
Larus ridibundus	Yes
Himantopus himantopus	Opposite
Recurvirostra avosetta	No clear pattern
Gallinago gallinago	Yes
Numenius arquata	No clear pattern
Scalopax rusticola	Yes
Tringa totanus	Yes
Ardea Cinerea	Yes
Botaurus stellaris	No clear pattern
Bubulcus ibis	Yes
Egretta garzetta	No clear pattern
Nycticorax nycticorax	Opposite
Ciconia ciconia	Yes
Ciconia nigra	Yes
Platalea leucorodia	No clear pattern
Columba oenas	Yes
Columba palumbus	Yes
Alcedo atthis	Yes
Upupa epops	Yes
Clamator glandarius	No clear pattern
Accipiter gentilis	Opposite
Aquila chrysaetos	Yes
Buteo buteo	Yes
Buteo rufinus	Opposite
Circus aeruginosus	Yes
Circus cyaneus	Yes
Gyps fulvus	No clear pattern
Haliaeetus albicilla	Yes
Hieraaetus pennatus	Yes
Milvus migrans	Opposite
Milvus milvus	Yes
Falco cherrug	Opposite
Falco columbarius	Yes
Falco naumanni	Yes
Falco Peregrinus	Yes
Falco rusticolus	Opposite
Falco tinnunculus	Yes
Coturnix coturnix	No clear pattern
Grus grus	Yes
Otis tarda	Yes
Fulica atra	Yes
Gallinula chloropus	Yes
Rallus aquaticus	Yes
Alauda arvensis	No clear pattern
Calandrella rufescens	No clear pattern
Calandrella brachydactyla	Opposite
Lullula arborea	Yes
Bombacilla garrulus	No clear pattern
Corvus corone	No clear pattern

Appendix 1 *continued*

Species	Sedentary in the east and migratory in the west?
Corvus frugilegus	Yes
Corvus monedula	Yes
Emberiza cia	No clear pattern
Emberiza citrinela	No clear pattern
Emberiza schoeniclus	Yes
Milaria calandra	No clear pattern
Carduelis cannabina	Yes
Carduelis carduelis	Yes
Carduelis flammea	Opposite
Carduelis flavirostris	Yes
Carduelis spinus	Yes
Coccothraustes coccothraustes	Yes
Fringilla coelebs	Yes
Pyrrhula pyrrhula	No clear pattern
Serinus serinus	Yes
Hirundo rustica	Yes
Ptyonoprogne rupestris	No clear pattern
Anthus petrosus	Yes
Anthus pratensis	Yes
Anthus spinoletta	Opposite
Motacilla alba	Yes
Motacilla cinerea	Yes
Motacilla flava	Opposite
Passer hispaniolensis	Yes
Passer moabiticus	Opposite
Prunella modularis	Yes
Remiz pendulinus	Yes
Sturnus vulgaris	Yes
Acrocephalus melanopogon	No clear pattern
Cettia cetti	No clear pattern
Phylloscopus collybita	Yes
Regulus ignicapillus	Yes
Sylvia atricapilla	Yes
Sylvia melanocephala	Yes
Troglodytes troglodytes	Yes
Erithacus rubecula	Yes
Monticola solitarius	Yes
Oenanthe xanthoprymna	No clear pattern
Phoenicurus ochruros	Yes
Saxicola torquata	Yes
Turdus merula	Yes
Turdus philomelos	Yes
Turdus pilaris	Yes
Turdus torquatus	Opposite
Turdus viscivorus	Yes
Phalacrocorax carbo	No clear pattern
Phalacrocorax pygmeus	Opposite
Phoenicopterus ruber	Yes
Podiceps cristatus	Yes
Podiceps nigricollis	Yes
Tachybaptus ruficollis	Yes
Asio flammeus	Yes
Asio otus	Yes