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Insight

Changes in Mammalian Body Length over 175 Years—Adaptations to a Fragmented Landscape?

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ABSTRACT. The potential consequences of anthropogenic habitat fragmentation on species diversity and extinction have drawn considerable attention in recent decades. In many cases, traditional island biogeography theory has been applied to explain the observed patterns. Here, we propose that habitat fragmentation as a selective force can be traced in mammalian body length changes. By exploring historical sources, we are able to show that the body length of Danish mammals has altered over a period of 175 years, possibly in response to increasing habitat fragmentation. The rate of body length change was generally lowest in medium-sized mammals, and increased with both smaller and larger body mass. Small mammals have generally increased, whereas large mammals have decreased in length. In addition to habitat fragmentation, some species may experience other selective forces, such as traffic, and may be trapped in an evolutionary tug-of-war, where the selective forces pull in opposite directions.

INTRODUCTION

Over the last centuries, the landscape in Denmark has undergone substantial changes: today, it consists of large areas of open, cultivated land with a few, widely dispersed fragments of natural habitat (see Caspersen 2001). Great efforts are being made to analyze the possible effects of these landscape changes on wildlife.

The potential effects of habitat fragmentation are often investigated using traditional island biogeography theory (MacArthur and Wilson 1967). This theory predicts that larger islands (or landscape fragments) are inhabited by more species than are small islands or fragments. Empirical data from a number of studies have supported this relationship (e.g., May 1975, Gorman 1979). We obtained similar results in our field study on small mammals and habitat fragmentation, as we found species richness to be positively correlated to the size of the habitat fragment (Jensen et al. 1999). It was, however, also clear that the isolation effect was limited, and that rodents colonized fragments proportional to their density.

Low population variability (i.e., a relatively stable population size over time) and high population density are two factors of crucial importance for minimizing the risk of extinction. Both factors, however, are influenced by body mass. Populations of medium-sized animals are less variable in numbers (Pimm 1992), and are also capable of reaching higher maximum densities (Marquet et al. 1995, Silva and Downing 1995) compared with both smaller and larger animals. Therefore, these two factors combined suggest that populations of medium-sized animals are more stable and have higher densities compared with both smaller and larger animals, possibly because medium-sized animals seem capable of controlling more energy than smaller and larger animals (Damuth 1993). Consistent with this, animals with body masses of about 100 g have the smallest home ranges (Kelt and van Vuren 2001) and reach the highest population densities (Marquet et al. 1995). Marquet and Taper (1998) found that only such medium-sized animals were capable of sustaining viable populations on the smallest islands. Moreover, these authors provided some evidence for the validity of this relationship when extended from the evolutionary scale to the ecological scale, i.e., to cover, for example, habitat fragmentation. Reviewing contemporary rodent data, Adler and Levins (1994) found that, compared with mainland populations, rodents obtained on islands were heavier, and had higher population densities and more stable populations. The island populations also survived better, but had reduced reproductive output compared with mainland populations (Adler and Levins 1994).

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Straightforward deductions based on the studies mentioned above suggest that adaptation to an increasingly fragmented landscape may be evidenced by an increase in size (i.e., body mass or body length) in smaller mammals, and a decrease in larger mammals, while medium-sized mammals remain essentially unchanged. In other words, in a changing landscape, the mammalian species may either become extinct or go through changes in life history traits that will adapt them to the changed living conditions. Thus, in the present study, we investigate whether the Danish mammal community has altered size toward being medium sized, the size that seems the most beneficial when living on islands, and thus, probably also when living in habitat fragments. However, aside from the island effect, a number of other ecological factors may also act on body length, emphasizing or limiting the change in size, and we attempt to integrate some of these into our analyses and discussion. First, competitive niche differentiation may limit or direct the magnitude of size changes within guilds. Bowers and Brown (1982) used a within-guild size ratio of about 1.5 as a conservative indicator of competitive displacement. Thus, large deviations from this ratio may indicate changes in inter-specific competition within the guild. Second, the reproductive capacity in mammal species, and thus the ability of a species to colonize the habitat fragments, may be determined largely by body mass (Brown et al. 1993). Therefore, reproductive capacity may be another important selective force in the fragmented landscape, forcing mammal species toward a size that optimizes reproductive output. Finally, size-specific mortality caused by anthropogenic factors, such as traffic, may be another important parameter. In some mammalian species, a substantial portion of the population is killed by traffic (e.g., Göransson et al. 1978, Hauer et al. 2002). The risk of getting killed by traffic, however, decreases with running speed (Hels and Buchwald 2001), which in turn increases with body mass (Garland 1983). Thus, traffic may act on size too and may therefore be another important selective force, encouraging animals toward being larger.

METHODS

As we wanted to investigate size changes over time within the entire Danish mammal assembly, and to overcome the potential bias from site-specific measurements, we extracted our data from historical sources, i.e., scientific monographs. Using monographs alone also ensures homogenous and independent data for all species at a specific time.

We obtained species mean body length measurements of Danish mammals from historical sources covering approximately 175 years (Holten 1800, Melchior 1834, Wulff 1881, Winge 1908, Hvass 1969, 1972). Within species and within the time period covered in this study, we presuppose body length to correspond closely to body mass, and size and size changes therefore refer to either term.

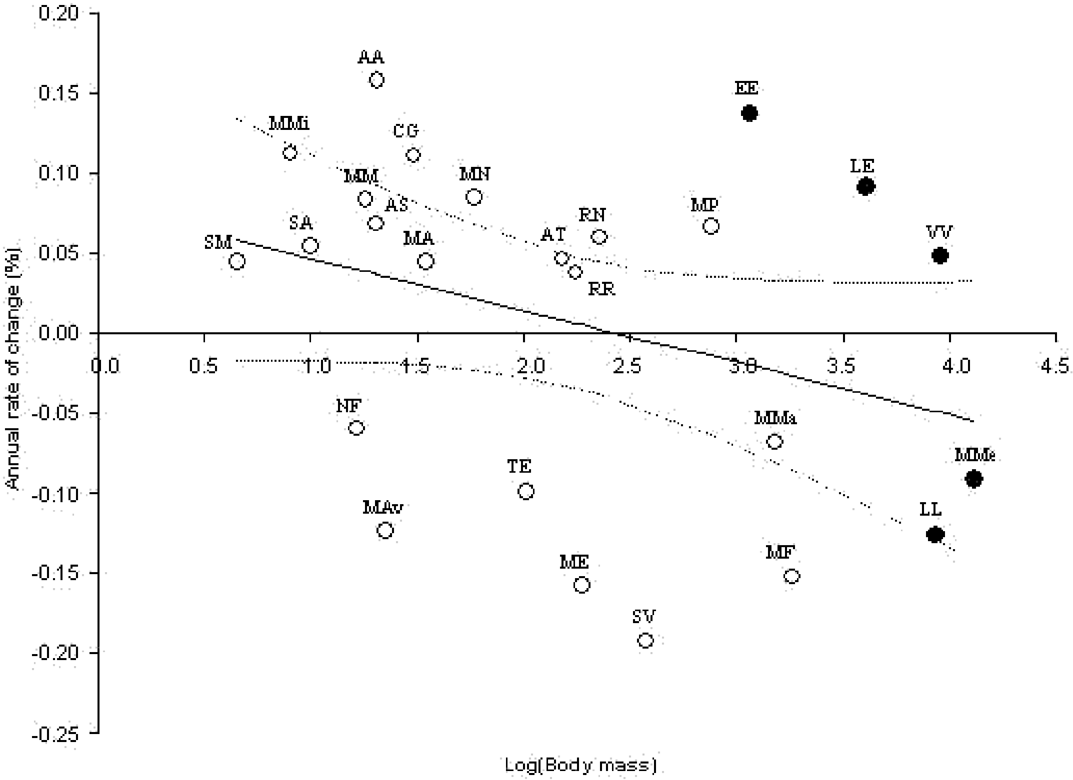
Measurements were converted into metric units. All measurements from species where nomenclature uncertainty existed were excluded. Only measurements from Danish mammals and only unique data, i.e. not repeated from earlier sources, were included in the analyses. In cases where body length was given as an interval, we used the interval mean as the average body length. The latter procedure was tested on independent length data from our rodent database and found to be reliable as a measure of average length. The average body length of adults did not differ significantly from the length of the interval mean in five rodent species (interval mean vs. average length: $R^2 = 0.98$, $P = 0.002$ for adults, 748 individuals).

We calculated the trend in the body length change as the annual rate of change (i.e., the slope of the linear regression on the body length for each species as a function of time, divided by the most recent body length measurements (the 1969 or 1972 data), multiplied by 100%). We then applied three successive general linear models. The first model described the rate of body length change as a result of present body mass (Appendix 1). The second model also included the impact of traffic as an independent variable (Appendix 1). Danish estimates of proportion of population killed in traffic only exist for badger (*Meles meles*; Aaris-Sørensen 1995); therefore, we supplemented this information with assessments from two neighboring countries, Sweden (Göransson et al. 1978) and Germany (Hauer et al. 2002), which most likely reflects the situation in Denmark. Hence, hedgehog (*Erinaceus europaeus*), brown hare (*Lepus europaeus*), red fox (*Vulpes vulpes*), otter (*Lutra lutra*), and badger were set to have high traffic mortality. Remaining species were set to have low traffic mortality. The average number of clutches per year (Appendix 1), was added as an independent variable in the last model.

RESULTS

An average of 4.36 (SD = 0.7) data points were used for each species to estimate the rate of body length change (Appendix 1).

Fig. 1. Annual rate of body length change in Danish mammals as a function of present body mass. Solid dots indicate species with high traffic mortality. Abbreviations used are EE - Hedgehog (*E. europaeus*); TE - Mole (*Talpa europaea*); NF - Water shrew (*Neomys fodiens*); SA - Common shrew (*Sorex araneus*); SM - Pygmy shrew (*S. minutus*); RN - Common rat (*Rattus norvegicus*); RR House rat (*R. rattus*); AS - Wood mouse (*A. sylvaticus*); AA - Striped mouse (*A. agrarius*); MM - House mouse (*Mus musculus*); MMi Harvest mouse (*Micromys minutus*); MA - Field vole (*Microtus agrestis*); CG - Bank vole (*Clethrionomys glareolus*); AT - Water vole (*Arvicola terrestris*); MAV - Hazel dormouse (*M. avellanarius*); SV - Red squirrel (*S. vulgaris*); LE - Brown hare (*L. europaeus*); VV - Red fox (*V. vulpes*); MMe - Badger (*M. meles*); MF - Stone marten (*Martes foina*); MMa - Pine marten (*M. martes*); MP - Polecat (*Mustela putorius*); ME - Stoat (*M. erminea*); MN - Least weasel (*M. nivalis*); and LL - Otter (*Lutra lutra*). Lines show linear regression with 95% confidence limits (Y = 0.08–0.03X)



When we plotted the rate of body length change against the present body mass of the 25 mammalian species (Appendix 1), we noted a negative trend (Fig. 1). Generally, only minor changes in body length occur around the intermediary body mass of approximately 280 g (Log_{10}(body mass) ≈ 2.44; $R^2 = 0.11$; Table 1), and both small and large mammals exhibit body length changes at higher rates compared with medium-sized mammals. Moreover, the smallest mammal species have generally increased in size, whereas the largest mammals have generally decreased. However, some species differ markedly from this general trend, and the relationship is not statistically significant (Table 1). When traffic-induced mortality was added to the model, a considerable part of the variation in body length change was explained ($R^2 = 0.27$; Table 1), and present body mass had a significant negative impact on the change rate, whereas traffic had a significant positive effect (Table 1). Adding the number of clutches per year for each species in the last model improved it and explained 40% of the variation in the rate of body length change, with significant positive estimates for high traffic-induced mortality and mean number of clutches, and significant negative estimates for body mass (Table 1).

Investigations of size ratio within the only proper guild in our data, the Mustelids, showed that, despite some displacement within the guild, no consistent changes in the potential niche overlap were found (Appendix 1). The average length ratio within the Mustelid guild over the 175-year period was 1.50 (SD = 0.25).

Table 1. Results from three successive general linear models of the annual rate of body length change (% change of present body length per year) in 25 Danish mammal species as a function of present body mass, traffic-induced mortality, and the mean number of clutches.

Independent variables	Source	d.f.	Sum of squares	Mean square	F value	Pr > F
Body mass	Model	1	0.03	0.03	2.77	0.110
	Error	23	0.23	0.01		
	Corrected total	24	0.26			
Body mass, traffic mortality	Model	2	0.07	0.03	3.97	0.034
	Error	22	0.19	0.01		
	Corrected total	24	0.26			
Body mass, traffic mortality, clutches	Model	3	0.10	0.03	4.68	0.012
	Error	21	0.15	0.01		
	Corrected total	24	0.26			

Note: All data used in these analyses are presented in Appendix 1. Independent variables shown in bold are significant (P<0.05; Type III sums of squares).

DISCUSSION AND SPECULATION

Using historical sources as we did may seem questionable. However, as we wanted a time span sufficient to allow micro-evolutionary changes to take place and as we were seeking a common explanation for the size changes for all mammals included in the analyses, we used only monographs to ensure a common size measurement methodology for the mammalian species in each source. Unfortunately, this limited the number of available sources. However, the sources we used seem reliable: all of them measured size according to body length (which we regard as much more reliable than, for example, body mass), and within most species measurements exhibit a relatively consistent pattern (Appendix 1). Therefore, we are confident that the body length changes observed in our study are not artifacts but actual changes. Most of the species-specific regression slopes (see Methods) are non-significant (Appendix 1), but this may be attributable to the small sample size. Nevertheless, the slope still expresses the general trend in size development. We also stress that the use of present body length and mass in our models is prone to increase the regression slope. However, the 25 mammalian species included here had an uneven representation of data points (Appendix 1) and, to ensure data integrity, present measurements were used instead of mean measurements.

Only two previous studies have been conducted on the long-term size changes in Danish mammals. They both reported skull size reductions in otters (Pertoldi et al. 1998, 2000), and stoats (Norup et al., personal communication). Both studies reported changes in mammal size consistent with the body length changes we observed. Thus, irrespective of the causes, mammal size does change over time, and such changes must be considered when, for example, modelling future population developments.

We found no consistent deviations from the expected size ratio within the Mustelid guild. Within-guild competition is, however, only one of many factors (e.g., density dependence, climatic parameters, hunting practices, etc.) that might affect mammalian body length. Thus, acknowledging the shortcomings and pitfalls of our idea, including the long list of other parameters that affect body length and which were omitted from our analyses, the data presented here must be interpreted with great caution until they can be supported by other sources. Nevertheless, at least two interesting, testable deductions can be made.

First, Danish mammals appear to be adapting to a landscape characterized by reduced or fragmented resources by altering their size toward a medium size. Such a directional size change has been previously observed on real islands (Lomolino 1985, Adler and Levins 1994), and is referred to as the "island rule" (van Valen 1973) or "island syndrome" (Adler and Levins 1994). Aside from the advantage of a lower risk of extinction (see Introduction), medium-sized mammals may also gain reproductive advantages compared with both smaller and larger animals (Brown et al. 1993). In our analyses, high reproductive capacity seems to compensate for the effect of body mass, probably because high reproductive capacity improves the chances of colonizing fragments. In this respect, it is noteworthy that increased size within a given species often increases its reproductive output (e.g., Ims 1987) whereas, across species, medium-sized mammals have a higher reproductive output than smaller or larger mammal species (Brown et al. 1993). Thus, the opposing effects of body mass and reproductive output in our data may indicate a trade-off between adapting to life within the fragments and the ability to colonize these fragments. However, being correlated to some extent, the occurrence of both body mass and reproductive capacity in the same model can be seen as questionable. Additionally, the species-specific dispersion strategies of the 25 mammalian species, and their potential variation over the 175-year period, preclude further deductions.

Still, medium-sized animals seem, in general, to fare better than smaller or larger animals on islands or in habitat fragments. Some of the species included in our analyses (e.g., red fox, badger, and brown hare) are habitat generalists and may, thus, be less influenced by fragmentation than the habitat specialists. Habitat specialists usually live within habitat fragments, whereas generalists live between fragments. Nevertheless, important life history events, such as reproduction, may still be associated with specific habitat fragments, and habitat generalists are therefore most likely also affected by habitat fragmentation. Moreover, the classification of mammal species into those living within fragments and those living between fragments simply mirrors the effect of body mass, as the smaller species live within fragments, and the larger species between fragments.

Second, some mammalian species may be subjected to contrasting selective forces of habitat fragmentation and traffic. Habitat fragmentation and the island rule may push mammals toward an intermediary size, whereas traffic may push them toward being larger, and hence, for the larger mammals, in opposition to the island rule. The risk of getting killed by traffic decreases with increased running speed (Hels and Buchwald 2001) which, in turn, increases with body mass (Garland 1983). Traffic as selective force may therefore increase size. Species such as the hedgehog, brown hare, red fox, otter, and badger, which suffer from high traffic-induced mortality, may be trapped in an evolutionary tug-of-war. The selective forces of habitat fragmentation and traffic pull in opposite directions but, given that traffic seems to be the strongest selective force, we expect the size distribution of these species to be skewed toward larger sizes.

In conclusion, our analyses suggest that the island effect is discernable in the historical data. Whether body length changes reflect true evolutionary processes or displacements in the frequencies of ecotypes within species remains unclear. Our analyses, however, also suggest that body length and body length changes over time may allow us to pinpoint species that are unable to keep track of their changing environment through micro-evolutionary adaptations and that are, therefore, in need of extraordinary conservation initiatives. These simple measurements may therefore become useful tools in the framing of tomorrow's conservation strategies in industrialized countries. However, further proof is needed and, therefore, we strongly encourage scientists in other countries to conduct similar analyses of their national data.

Responses to this article can be read online at:
http://www.consecol.org/vol7/iss2/art6/responses/index.html

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APPENDIX 1. Body length measurements (cm), and summarized statistics of 25 Danish mammal species from 1800 to 1972

	Holten (1800)	Melchior (1834)	Wulff (1881)	Winge (1908)	Hvass (1969, 1972)	Body mass[a]	Slope	SE	R^2	*P* value	Mean no. of clutches[b]	Size-dependent mortality[c]
Badger	109.85	111.15	95.46	87.00	100.50	13000.00	-0.09	0.07	0.37	0.283	1.0	High
Bank vole	11.77	13.51	13.08	12.70	15.60	30.00	0.11	0.05	0.66	0.095	4.5	Low
Brown hare	54.92	65.39	65.39	70.00	66.50	4000.00	0.09	0.05	0.50	0.182	3.5	High
Common rat		41.19	41.85	39.70	45.25	225.00	0.06	0.05	0.45	0.330	8.0	Low
Common shrew	10.46		9.57	10.25	11.60	10.00	0.06	0.06	0.29	0.459	2.5	Low
Field vole		14.06	13.73	12.90	15.05	35.00	0.05	0.06	0.19	0.559	4.5	Low
Harvest mouse		10.46	12.42	10.85	12.85	8.00	0.11	0.08	0.51	0.288	3.0	Low
Hazel dormouse	17.00	15.69	15.04	13.80	14.10	22.50	-0.12	0.04	0.80	0.040	2.0	Low
Hedgehog	20.92	24.85		25.10	29.00	1150.00	0.14	0.04	0.85	0.076	2.0	High
House mouse	14.38	15.69		15.10	17.60	18.00	0.08	0.04	0.69	0.172	6.0	Low
House rat	36.62	40.87	40.54	36.80	41.55	175.00	0.04	0.04	0.20	0.454	4.0	Low
Least weasel	19.62	23.54	22.88	22.55	24.50	58.00	0.08	0.04	0.57	0.140	1.5	Low
Mole		18.31	15.69	15.50	15.90	102.50	-0.10	0.07	0.47	0.314	2.0	Low
Otter		125.54		103.00	107.50	8500.00	-0.13	0.10	0.61	0.428	1.0	High
Pine marten		78.46	70.62	69.00	71.25	1500.00	-0.07	0.05	0.43	0.343	1.0	Low
Polecat	47.08	54.92	61.46	58.00	54.00	750.00	0.07	0.08	0.20	0.451	1.0	Low
Pygmy shrew			9.15	8.40	9.33	4.50	0.04	0.10	0.16	0.742	3.0	Low
Red fox	104.62	104.51		110.00		9000.00	0.05	0.02	0.90	0.210	1.0	High
Red squirrel	49.69	45.77	44.46	39.00	37.50	372.50	-0.19	0.03	0.92	0.011	1.5	Low
Stoat	41.85	37.27	37.27	29.60	33.50	187.50	-0.16	0.08	0.58	0.134	1.0	Low
Stone marten		83.69		69.00	69.50	1800.00	-0.15	0.09	0.76	0.326	1.0	Low
Striped mouse		14.71	15.04	15.90	18.65	20.50	0.16	0.04	0.90	0.050	2.5	Low
Water shrew		15.37	15.69	12.75	14.60	16.50	-0.06	0.10	0.14	0.622	2.5	Low
Water vole	28.77	25.38	24.19	27.00	30.50	150.00	0.05	0.07	0.14	0.535	7.0	Low
Wood mouse	15.69	15.91	19.62	17.90	17.30	20.00	0.07	0.07	0.25	0.395	2.5	Low

Notes: [a] In grams, based on Hvass (1969, 1972). [b] Based on Muus (1991). [c] Based on Göransson et al. (1978), Aaris-Sørensen (1995), Hauer et al. (2002).

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