Recent Changes in Body Size of the Eurasian Otter *Lutra lutra* in Sweden

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Received: 18 February 2009 / Revised: 21 April 2009 / Accepted: 18 May 2009 / Published online: 9 July 2010

Abstract We studied geographical and temporal body size trends among 169 adult museum specimens of the Eurasian otter (*Lutra lutra*) collected in Sweden between 1962 and 2008, whose sex, year of collection, and locality were known. Skull size and body mass increased significantly in relation to the year of collection, and skull size (but not body mass) was significantly and negatively related to latitude, contrasting Bergmann's rule and the trend found for Norwegian otters. Latitudinal differences in body size between the two countries may be due to differences in food availability. The temporal increase in body size among Swedish otters resembled that observed for Norway otters, though Swedish otters are smaller with respect to their Norwegian counterparts. Latitude and year represent a combination of environmental factors, including ambient temperature in the year of collection as well as the number of days of ice coverage. We replaced the above factors with mean annual temperature or the number of days of ice coverage, and found that each of these factors explains a similar proportion of the variation in body size as did latitude and year. We hypothesize that this temporal increase in body size is related to a combination of factors, including reduced energy expenditure resulting from increasing ambient temperature, and increased food availability from longer ice-free periods.

Keywords Eurasian otter · *Lutra lutra* · Sweden · Body size · Ambient temperature · Ice coverage · Food availability · Global warming

INTRODUCTION

During the past decades, it has become apparent that an animal's body size can vary temporally within a range of

several decades (reviewed by Millien et al. 2006). Since all the observed temporal changes are not the results of controlled experiments, we can only speculate regarding the factors causing such changes. Several authors have nevertheless suggested various possibilities: e.g., that recent changes in body size were caused by predation (in the great tit *Parus major*; Gosler et al. 1995), global climate change (in the wood rat *Neotoma*; Smith et al. 1998), or food availability (in otters *Lutra lutra*, lynx *Lynx canadensis* and other carnivores; Yom-Tov 2003; Yom-Tov et al. 2006, 2007).

The Eurasian otter, *L. lutra*, a medium-sized predator, has a wide range in the Palearctic region, and its ecological equivalent, the North American river otter *Lontra canadensis*, is widespread in the Nearctic region. Both species vary in body size across their distribution range, thus demonstrating an ability to adjust body size to geographical conditions, presumably in reaction to varied environmental selection pressures. Scholander (1956) claimed “the American otter... defies Bergmann's rule by getting smaller going north.” However, Yom-Tov et al. (2006) have shown that body size of the Eurasian otter in Norway tends to be larger in the north than in the south, and thereby conforms to Bergmann's rule. Meiri et al. (2007) confirmed this trend over the Palearctic region. Yom-Tov et al. (2006) showed that body size of the Eurasian otter in Norway increased during the last third of the twentieth century and related this trend to increased food availability from fish farming, and possibly also to energy saving due to elevated sea temperatures. Pertoldi et al. (1998) found a negative correlation between year of collection and skull size among Danish otters, and attributed this trend to various factors, such as pollution, human activity, food shortage, and habitat fragmentation.

Norway and Sweden have a long common border and their faunas have much in common. Nevertheless, the main

otter habitats of the two countries differ in several ways. In Sweden most otters live inland along freshwater sources, feeding mainly on freshwater fish (Bister and Roos 2006), while the otter in Norway, both historically (Johnsen 1928) and recently (Heggberget et al. 2007), has been more common on the coast, feeding mainly from the sea (Heggberget 1993). Moreover, latitudinal winter temperature clines are steeper in Sweden (Tveito et al. 2000) than along the Norwegian Atlantic coast, inhabited by the otters (Yom-Tov et al. 2006). Hence, during winter access to fish inhabiting freshwater lakes is limited in Sweden where ice covers the lakes for part of the winter, whereas most Norwegian otters have access to ice-free waters.

A body of evidence is accumulating, implicating global climate being modified by human activities (Räisänen et al. 2003). It is reasonable to assume that, in Sweden, the increase in ambient temperature during the second half of the twentieth century would reduce the period of winter ice coverage on internal lakes and other water bodies, thus increasing access to food for otters. Such a reduction has been observed on lakes in both the south and north of Sweden (Ask and Westerberg 2008). We predicted that this increased food availability would positively affect the

otters' body size. Further, because the period of ice coverage increases from south to north, we predicted that in Sweden otters' body size would decline from south to north, contrary to Bergmann's rule. We tested these predictions by relating body size of museum specimens of Swedish otters to several environmental parameters, and compared the results to those obtained from Norwegian otters. This article reports our findings, discussing possible explanations for observed body size variations.

ANIMALS: MATERIALS AND METHODS

Skulls of 169 otters (60 females, 109 males) were measured at the Swedish Museum of Natural History (NRM), Stockholm. Skulls of young specimens approximately less than 2 years old (open sutures between the bones of the skulls) were not included in the sample. The specimens were adults of known sex and with data on latitude, longitude, and year of collection. Otters were collected between 1962 and 2008 from all over Sweden (Fig. 1), between 55.6–67.7°N and 11.1–23.5°E. Using digital calipers we measured the maximal width of the zygomatic

Fig. 1 Locations of the studied otters

breadth (ZB) to an accuracy of 0.01 mm. In mammals, ZB is usually correlated with body weight and length (Creighton 1980; Johnston 1991; Pertoldi et al. 1998). Most (157) of the carcasses had been weighed either in the laboratory or by the hunters, but on different balances.

Temperature and ice coverage data were obtained from the Swedish Meteorological and Hydrological Service (SMHS; <http://www.smhi.se/cmp/jsp/polopoly.jsp?d=6413&sv>). For calculating long-term temperature trends across Sweden we used mean annual data from homogenized temperature series, which were taken from 37 stations around Sweden.

For each specimen we fitted a value of mean annual temperature of the year it was collected. These temperature data are for one-degree square (geographical degrees) and were kindly provided by Dr. Mark Lomas, Sheffield University. These are mean annual temperature data for each degree-square and cover the period 1900–2002. For otters collected during 2003–2008 we used mean annual temperature of 2002 of the degree square from which they were collected and corrected annual values by adding 0.123°C for each year after 2002. This value (0.123°C) is the average increase in ambient temperature across Sweden obtained from the SMHS data above (see “Results”).

We suggest that ice coverage determines the access of otters to the aquatic animals that form their main food source. Data on ice coverage were obtained for 744 lakes for the period 1960–2007. These data include the first date that ice covered the lake and the date when the ice melted. From these data we calculated the total number of days of ice coverage for every lake. We then used a multiple regression analysis to create a model that predicts the number of days of ice coverage, taking into consideration latitude, longitude, and year (Ice coverage (days) = $374.3096 + 10.2817 \times \text{latitude} - 3.2930 \times \text{longitude} - 0.4393 \times \text{year}$). We used the model to estimate the number of days of ice coverage for all otters in our sample.

Statistics

Both ZB and body mass data were normally distributed. We examined the effects of sex (categorical variable), year of collection, latitude, and longitude, and their two-way interactions on ZB and body mass by running multiple regressions using JMP (ver. 5.1, SAS Inc.).

The factors latitude, longitude, and year represent a combination of environmental factors, including ambient temperature in the year of collection as well as the number of days of ice coverage. In order to test the effect of ambient temperature and ice coverage on ZB and body mass we ran a multiple regression as above, in which we retained sex as an independent factor but replaced year, latitude, and longitude with ambient temperature, and the

number of days of ice coverage as independent factors. The data on homogenized ambient temperature represent the temporal change in temperature in Sweden during the study period. Latitude and longitude may represent several other factors, including a change in food availability, but we have no direct data on this factor. However, the length of the period of ice coverage is probably a good proxy for food availability during winter.

We used the above ZB measurements from Sweden in order to compare the temporal increase of otters in Sweden to that of Norway. Details on Norwegian data set (1,146 otters) are provided in Yom-Tov et al. (2006).

RESULTS

Mean annual temperature during the study period (1964–2008) in Sweden significantly rose by about 1.8°C ($F_{(1,42)} = 18.1$, $R^2 = 0.30$, $P = 0.0001$). Since 2001 mean annual temperature increased linearly at a mean rate of 0.123°C/year.

Body mass was significantly related to ZB ($F_{(1,144)} = 198.7$, $R^2 = 0.58$, $P < 0.0001$), indicating that ZB is a good predictor of body size.

The number of days of ice coverage was significantly related to latitude, longitude, and year (ice days = $493.553 + 10.096 \times \text{latitude} - 2.847 \times \text{longitude} - 0.496 \times \text{year}$; $F_{(3,9491)} = 4606.0$, $R^2 = 0.59$, $P < 0.0001$).

The same pattern was seen for mean annual temperature, which also was significantly related to latitude ($R^2 = 0.77$, $P < 0.0001$), longitude ($R^2 = 0.08$, $P = 0.0002$), and year ($R^2 = 0.05$, $P = 0.0055$). These results indicate the well-known effect of latitudinal and temporal changes on temperature. The significant relationship between temperature and longitude is probably due to the fact that, in Sweden, high longitudes occur in high latitudes. The number of days of ice coverage was significantly related to mean annual temperature ($R^2 = 0.89$, $P < 0.0001$).

Results of multiple regressions showed that males were significantly larger than females and that latitude had a significant negative effect on ZB, thus indicating that skull size (but not body mass) decreased with latitude (Table 1). The full factorial models for ZB and body mass accounted for 48.1% and 43.2% of the variance in ZB and body mass, respectively (ZB: $F_{(4,153)} = 35.5$, $P < 0.0001$; Body mass: $F_{(4,152)} = 29.0$, $P < 0.0001$; Table 1). Year had a significant positive effect on both ZB and body mass, indicating that body size increased during the study period. Partial regressions revealed that sex accounted for most of the variation in ZB and body mass (43.5% and 37.5%, respectively) and year, latitude, temperature, and ice coverage explained a relatively smaller but significant proportion of the overall variation. Year accounted for 4.6%

Table 1 : Effect of sex, year, latitude, and longitude on ZB and sex and year on body mass

Parameter estimates				
Term	ZB		Body mass	
	<i>t</i> value	<i>P</i> value	<i>t</i> value	<i>P</i> value
Intercept	−0.60	0.5476	−3.25	<u>0.0014</u>
Sex	10.85	<u><0.0001</u>	9.57	<u><0.0001</u>
Year	2.72	<u>0.0073</u>	3.67	<u>0.0003</u>
Latitude	−2.97	<u>0.0034</u>	−1.33	0.1857
Longitude	0.76	0.4485	0.87	0.3878

The full factorial models (ZB: $F_{(4,153)} = 35.5$, $P < 0.0001$; body mass: $F_{(4,152)} = 29.0$, $P < 0.0001$) accounted for 48.1% and 43.2% of the variance in ZB and body mass, respectively. Significant results are underlined. All interactions were not significant and are not included in this analysis

and 8.1% of the variation in ZB and body mass, respectively, and latitude accounted for 5.4% of the variation in ZB, but was not significantly correlated with body mass. The calculated increase in ZB and body mass between 1962 and 2008 of a male from 60°N, 17°E was 3.5% (from 68.2 to 70.5 mm) and 32.2% (from 5538 to 7426 g), respectively.

In a second set of regressions we replaced latitude, longitude, and year with (1) annual temperature (Table 2) or (2) the estimated local annual number of days of ice coverage (Table 3). Our results showed that sex and ambient temperature accounted for 47.0% and 39.6% of the variance in ZB and body mass, respectively (ZB: $F_{(2,155)} = 68.8$, $P < 0.0001$; Body mass: $F_{(2,154)} = 50.6$, $P < 0.0001$). Sex and number of days of ice coverage accounted for 46.6% and 39.0% of the variance in ZB and body mass, respectively (ZB: $F_{(2,155)} = 67.8$, $P < 0.0001$; Body mass: $F_{(2,154)} = 49.2$, $P < 0.0001$). Partial regressions revealed that sex accounted for most of the variation in ZB (43.5%) and body mass (37.2%), while temperature accounted for 7.9% and 3.7% of the variation in ZB (Fig. 2a) and body mass (Fig. 2b), respectively, and ice

Table 2 Effect of sex, and ambient temperature on ZB and body mass

Parameter estimates				
Term	ZB		Body mass	
	<i>t</i> value	<i>P</i> value	<i>t</i> value	<i>P</i> value
Intercept	145.47	<u><0.0001</u>	18.80	<u><0.0001</u>
Sex	10.92	<u><0.0001</u>	9.57	<u><0.0001</u>
Temperature	3.65	<u>0.0004</u>	2.45	<u>0.0155</u>

ZB: $F_{(2,155)} = 68.8$, $P < 0.0001$; body mass: $F_{(2,154)} = 50.6$, $P < 0.0001$. The models accounted for 47.0% and 39.6% of the variance in ZB and body mass, respectively. Significant results are underlined

Table 3 Effect of sex and the number of days of ice coverage on ZB and body mass

Parameter estimates				
Term	ZB		Body mass	
	<i>t</i> value	<i>P</i> value	<i>t</i> value	<i>P</i> value
Intercept	93.15	<u><0.0001</u>	13.97	<u><0.0001</u>
Sex	10.92	<u><0.0001</u>	9.54	<u><0.0001</u>
Ice coverage	−3.48	<u>0.0006</u>	−2.06	<u>0.0406</u>

ZB: $F_{(2,155)} = 67.8$, $P < 0.0001$; body mass: $F_{(2,154)} = 49.2$, $P < 0.0001$. The models accounted for 46.7% and 39.0% of the variance in ZB and body mass, respectively. Significant results are underlined

coverage accounted for 7.2% and 2.7% of the variation in ZB and body mass, respectively (Fig. 2c, d).

Comparison of ZB among otters between Sweden and Norway showed that Swedish otters were smaller than their Norwegian counterparts (for females: $t_{(38,455)} = -8.4$, $P < 0.0001$, for males: $t_{(80,691)} = 12.7$, $P < 0.00001$; mean ZB was 68.17 and 64.75 mm for females and 73.85 mm and 69.41 mm for males, in Norway and Sweden, respectively, differences of 5.4% and 6.4%). Otters in both countries showed an increase in size for the study period (1962–2004), and there was no difference in the effect of year on ZB between the countries (Table 4).

DISCUSSION

We found that body size of the otter in Sweden varied both geographically and temporally, being smaller toward the north but increasing overall during the past half century in relation to an observed increase in ambient temperature. While year was significantly related to both body parameters, latitude was significantly related only to ZB. We suggest that the reason for the difference in the proportion of variation explained by year and latitude between ZB and body mass is that adult skeletal parts, including ZB, are determined during the entire growth period of an animal, whereas body mass also reflects the conditions experienced by an animal shortly before its death and might reflect the season of the year rather than the year itself.

Both year and latitude are proxies for a variety of factors that are poorly understood, and we can only speculate regarding these factors. The year effect may include the recent increase in ambient temperature resulting in less energy expenditure, as well as changes in food availability resulting from a longer growing season and shorter duration of ice cover due to increased temperature. The latitude effect may include, in addition to the temperature gradient, differences in prey species composition and density. Prey availability for otters is more stable and predictable in the

Fig. 2 **a** Partial regression plots for ZB (controlled for sex; slope = 0.0250, $P = 0.0003$) as a function of ambient temperature. **b** Partial regression plots for body mass (controlled for sex; slope = 1.5257, $P = 0.0152$) as a function of ambient temperature. **c** Partial regression plots for ZB (controlled for sex; slope = 0.0161, $P = 0.0007$) as a function of ice coverage (days). **d** Partial regression plots for body mass (controlled for sex; slope = 1.9683, $P = 0.0401$) as a function of ice coverage (days)

Table 4 Effect of country of origin, year of collection, and their interaction on ZB corrected for sex and latitude; $F_{(3,1260)} = 33.7$, $P < 0.0001$

Term	ZB	
	t value	P value
Intercept	-1.15	0.2491
Year	3.66	<u>0.0003</u>
Country	-8.70	<u><0.0001</u>
Year $\times$ country	0.82	0.4127

Significant results are underlined

south than in the north, as the lakes and rivers are frozen for a longer period in the north of Sweden, while the waters may be ice-free at all times in parts of southern Sweden (Raab 1995; Ask and Westerberg 2008). These factors indicate that (at least during winter) more prey, including frogs, birds, and crayfishes, are available in the south than in the north.

In a second set of tests we replaced year, latitude, and longitude with data of (1) annual ambient temperature in Sweden and (2) the estimated local annual number of days of ice coverage. We found that for these two factors the proportion of variation in body size explained by the first

set of variables (sex, latitude, longitude, and year; 48.1% for ZB) was very similar to that explained by sex and annual temperature (47.0%) and sex and days of ice coverage (46.7%). For body mass, the proportions of the variation explained by these sets of variables were 43.2, 39.6, and 39.0%, respectively; e.g., latitude and year explained just a little more of the variation than did temperature and ice coverage.

Partial regression plots revealed that ambient temperature and ice coverage explained a similar proportion of variation in skull size as did year and latitude. However, year and latitude explained about 4% less of variation in body mass as did temperature and ice coverage. Body length and mass at adulthood provide different reflections of environmental change. In the sea otter *Enhydra lutris*, body length probably reflects conditions experienced in the early years of life, while body mass represents recent nutritional status (Laidre et al. 2006). The fact that in our study ambient temperature and ice coverage affected ZB more than body mass may indicate that conditions during the period of prenatal or postnatal growth (a period that often coincides with the melting of ice on northern lakes in Sweden) are important in determining body size. However, body mass is highly variable and dependent on daily

changes, and since many of the otters in our sample had not died during periods of ice coverage we do not expect this factor to be related to body mass.

Below we discuss the possible effects of each of these factors as well as that of environmental pollutants, and also consider the possible effects of Norwegian otters that were introduced to Sweden.

Temperature increase

Partial regressions showed that ambient temperature explained significant proportions of the variation in body size. This indicates that increase in temperature is an important factor responsible for the temporal increase found in body size of the otter in Sweden.

Increase in temperature can affect otters both indirectly, through its effect on food, and directly, through its effect on energy requirements for maintenance. The indirect effect may take place by increasing Net Primary Productivity (NPP) or by affecting ice-cover on fresh-water bodies and thus increasing access to fish and invertebrates living in these water bodies. Raab (1995, p. 11) noted that mean annual temperature has a considerable effect on NPP in Sweden, where NPP increases from 500 g/m²/year at 0°C to 1000 g/m²/year at 7°C. The effects of increased fresh-water temperatures on prey biomass are more difficult to predict, as this will favor temperate water species and disfavor coldwater species. However, a moderate increase in water temperature may increase productivity, and thus food availability, for the otter.

We have previously discussed the importance of ambient temperature for the metabolism of otters and found that within an ambient temperature range 3–18°C, a 1°C increase in ambient water temperature decreases oxygen consumption by 6.4% and 12.4% of resting metabolic rate (Yom-Tov et al. 2006). Examination of an homogeneous temperature series revealed that the annual temperature increased by 0.3–1.0°C in different parts of Fennoscandia during the twentieth century (Tveito et al. 2000), and during our study period mean annual temperature in Sweden rose by 1.7°C. Hence, it seems that the observed increase in ambient temperature also had a direct positive effect on the size of otters in Sweden.

Only future research will enable to determine what is the contribution of each of the above effects to the increase in otters' body size.

Geographical trend in body size

We found that otters are smaller in the north of Sweden compared to the south. This is in contrast to what was found for otters in Norway (Yom-Tov et al. 2006). Meiri et al. (2007) reported a positive trend in body size of otters

in the Palearctic region, but this trend is probably due to the very small otters in the south of its distribution area, and not a result of a steadily increasing cline (S. Meiri, pers. comm.). McNab (1971) showed that the North American river otter defies Bergmann's rule within two latitudinal ranges (below 30°N and between 46 and 60°N), but conforms to it within another latitudinal range (30–45°N). McNab (1971) claimed that this pattern is due to resource availability. Ice cover is an important factor determining prey availability during winter. The lakes and rivers are frozen for a long period in winter in the north of Sweden, while the waters may be open at all times in parts of southern Sweden (Raab 1995; Ask and Westerberg 2008) as is also the case along the entire Norwegian Atlantic coast. Hence, access to prey is more stable and predictable in southern than in northern Sweden.

Prey species composition and species richness differ geographically within Sweden (Gustafson and Ahlen 1996; Rask et al. 2000). This is likely to influence feeding energetics, as Eurasian otters tend to catch slow-moving, demersal fish species (Erlinge 1968; Kruuk 1995). However, data suitable for analysis of prey composition or density were not available for this study.

Environmental pollutants

Environmental pollutants may also contribute to the observed trend in body size. Roos et al. (2001) analyzed the population trend in Swedish otters in relation to environmental pollutants. The dramatic decrease in population size during the 1960–1980s coincided with an increased occurrence of PCBs in the environment including otters in the first part of the period. In general, the concentrations in otters were higher in southern Sweden than in the north. Since the 1990s the otter population in Sweden has been increasing while the contaminant levels have decreased. The concentrations of PCB have thus decreased in otters in the south and are now similar to those in otters from other parts of Sweden, albeit with a quite large variation (A. Roos, unpublished data). The otter population is currently strongly increasing in both numbers and distribution (A. Roos, unpublished data). PCBs might have an effect on the growth patterns of mammals (e.g., Sagiv et al. 2007; Bechshøft et al. 2008), and it is reasonable to assume that the size of Swedish otters has been suppressed by high PCB loads. The detected recent increase in otter body size could thus be a result of lower pollution levels during the third part of the twentieth century. However, this relationship cannot be proven from the present dataset.

If PCBs have had an effect of otter size in Sweden, as suggested above, then one would assume that otters in the generally less polluted north should be larger than those in the south. This is opposite, however, to the geographical

size trend we detected, suggesting that the possible pollution effect is only one of the factors that affect body size; and that food availability and climate change may also contribute to the observed trend of body size increase.

Restocking Swedish otter populations

A restocking program for otters in Sweden was initiated in the 1980s in order to counteract the observed dramatic decline in population size. A total of 54 otters originating from northern Norway were released into two areas in southern Sweden (47 at one site and 7 at another) between the years 1987 and 1992 (Sjöåsen 1997). Since Norwegian otters are larger in the north than in the south and overall are generally larger than Swedish otters, this could have interfered with the natural processes of evolution of size in relation to environmental conditions in Swedish otters. All the released otters originated from northern Norway. However, Arrendal et al. (2004) evaluated the genetic consequences of the translocations and concluded that the genetic effects of the translocations appeared to be restricted to areas in the immediate vicinity of the release sites. Therefore, it is unlikely that these translocations would have had any effect on the body size of southern Swedish otters. Besides, all otters were released to the south of Sweden, and since otters from the north also have increased in size over time, one can rule out a possible impact from released animals.

Comparison between Swedish and Norwegian otters

Body size of Swedish otters has increased linearly during the last four decades, at a rate of increase not differing from that reported for Norwegian otters (Yom-Tov et al. 2006). In Norway we suggested that this increase in size is related to increased food availability from fish farming, and possibly also to energy saving due to slightly elevated sea temperatures. In Sweden the distribution of otters is not mainly confined to coastal marine habitats as in Norway, but is now mostly distributed in the inland freshwater areas, throughout most of the country (Roos et al. 2001). In Sweden the otter mainly preys on fish (Erlinge 1968; Bister and Roos 2006). Fish farming in Sweden (Holmquist and Funcke 2006) is minor compared to Norway (Kjørhaug 2006a, b), and the otter does not seem to be regarded as a serious problem for Swedish fish farmers (Bister and Roos 2006). Moreover, production of farmed fish did not increase in Sweden between 1988 and 2005 (Holmquist and Funcke 2006). Therefore, it is unlikely that increased food availability from fish farms is the explanation for the otters' increased body size in Sweden, in contrast to its influence in Norway.

In summary, we found that skull size and body mass of the otter in Sweden are related to either mean annual temperature or the number of days of ice coverage, and that each of these factors explains a similar proportion of the variation in body size as did latitude and year. We hypothesize that this temporal increase in body size is related to a combination of factors, including reduced energy expenditure resulting from increasing ambient temperature and increased food availability from longer ice-free periods.

Acknowledgments Thanks are due to Olavi Grönwall for his warm hospitality to YYT and SYT during their visit to the NRM and to Per Ericson for his valuable support. We are grateful to Eli Geffen for advice and comments, to Naomi Paz for editing this article, and to two anonymous reviewers for their helpful suggestions. YYT and SYT would like to thank Nick Davies for his hospitality during their sabbatical in Cambridge, England. We are grateful to Else-Marie Wingqvist of the Swedish Meteorological Service and to Mark Lomas of Sheffield University for their help in obtaining climate data. We acknowledge the financial support of a SYNTHESYS grant to YYT (SE-TAF-1844) made available by the European Community Research Infrastructure Action under the FP6 Structuring the European Research Area Programme, and the Israel Cohen Chair of Environmental Zoology to YYT.

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