

Born to be wild? Response of an urban exploiter to human-modified environment and fluctuating weather conditions

Geneviève Turgeon, Eric Vander Wal, Ariane Massé, and Fanie Pelletier

Abstract: Human-driven environmental changes affect behavior, morphology, life history, and population dynamics of wild species. Artificial food sources in anthropogenic environments benefit some species and may lead to faster somatic growth and larger body size, which affects survival and reproduction, thus contributing to a species' success in modified environments. Using raccoons (*Procyon lotor* (L., 1758)) as a model, we documented age-specific body-mass pattern and evaluated the influence of human activities (human density, area with artificial food sources, edges of forested area bordering corn (*Zea mays* L.) fields) and weather (index of winter severity and mean annual precipitation) on body-mass variation at multiple spatial scales. The effect of human-driven changes on raccoon mass varied with age, sex, and spatial scale, suggesting that anthropogenic changes affect raccoons differentially according to gender and life stages. Human activity had consistently opposing effects between the sexes. Weather covariates represented >50% of the total variance in body mass explained by our models. Previous winter severity and mean annual precipitation affected body mass negatively and positively, respectively. Our results emphasize the importance of multiscale, sex- and age-specific analyses when studying influences of human activity on wildlife.

Key words: *Procyon lotor*, raccoon, anthropogenic diet, agricultural subsidies, wild population, urban exploiter, winter severity, annual precipitation.

Résumé : Les changements anthropogéniques influence le comportement, la morphologie, l'histoire de vie et la dynamique de population des espèces sauvages. Les sources de nourriture artificielles, provenant des ordures et de l'agriculture, peuvent être bénéfiques pour certaines espèces, menant à une croissance corporelle rapide, à une masse plus grande affectant ultimement la survie et la reproduction. Nous avons documenté les patrons de masse âge-spécifique et évalué l'importance relative de l'activité humaine (densité de population humaine, aires avec source de nourriture artificielle, densité de lisière forêt/champs de maïs (*Zea mays* L.)) et du climat (sévérité de l'hiver et moyenne des précipitations) sur la masse corporelle du raton laveur (*Procyon lotor* (L., 1758)) à plusieurs échelles spatiales. L'effet des changements anthropiques sur la masse des rats laveurs variait avec l'âge, le sexe et l'échelle, suggérant une influence différentielle selon le stade de vie. L'activité humaine avait un effet opposé selon le sexe. Les variables du climat expliquaient plus de la moitié de la variance totale des modèles. La sévérité de l'hiver précédent et les précipitations moyennes annuelles affectaient la masse négativement et positivement, respectivement. Ces résultats soulignent l'importance de faire des analyses âge-spécifiques et à plusieurs échelles pour évaluer l'influence de l'activité humaine sur les espèces sauvages.

Mots-clés : *Procyon lotor*, raton laveur, diète anthropique, agriculture, population sauvage, espèces urbaines, sévérité hivernale, précipitation moyenne annuelle.

Introduction

Global environmental changes are increasing, mainly due to human activity (Matson et al. 1997; Tilman and Lehman 2001). Human-driven changes such as fragmentation and climate change modify habitat quality, resource composition and availability, and as a result affect wild populations (Festa-Bianchet et al. 2011). Why do some species thrive in highly human-modified landscapes, while others go extinct when their habitat is affected by human activities? Despite anthropogenic activities predominantly negatively affecting wild species, an increasing number of species—mainly generalists (Dickman and Doncaster 1989; Andréon 1994)—are adapting to live in sympatry with humans, especially in urban and suburban landscapes (Ditchkoff et al. 2006). These species are known to reach higher densities in anthropogenic landscapes

than in their historical habitat (Dickman and Doncaster 1987; Fedriani et al. 2001; Withey and Marzluff 2009). Such high densities are likely caused by the presence of abundant artificial resources that are by-products of human activity, such as discarded foods or unused buildings (for a review see Bateman and Fleming 2012). Identifying how novel ecological factors emerging from human activities affect wild animals is critical to improve management of human-adapted abundant species and species of conservation concern (Bateman and Fleming 2012; Graser et al. 2012).

The link between artificial food sources and population density is well documented. For example, studies have shown that artificial food sources can buffer seasonal change in food resources thereby sustaining high population numbers (Bateman and Fleming 2012). Less well known, however, is the relationship between artificial

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G. Turgeon, E. Vander Wal, and F. Pelletier. Canada Research Chair in Evolutionary Demography and Conservation, Département de biologie, Université de Sherbrooke, 2500, boulevard de l'Université, Sherbrooke, QC J1K 2R1, Canada.

A. Massé. Direction de la biodiversité et des maladies de la faune, Direction générale de l'expertise sur la faune et ses habitats, Ministère des Forêts, de la Faune et des Parcs, 880, chemin Sainte-Foy, Québec, QC G1S 4X4, Canada.

Corresponding author: Geneviève Turgeon (e-mail: Genevieve.S.Turgeon@USherbrooke.ca).

food sources and phenotypic traits linked to fitness, such as body mass. Here research is sparse and oftentimes contradictory. For example, it has been shown for several species that individuals inhabiting urban areas or areas in close proximity to artificial food sources are heavier (Cypher and Frost 1999; Beckmann and Berger 2003; Wright et al. 2012). Conversely, body mass in other successful urban species appeared unrelated or negatively affected by human activity (Hungerford et al. 1999; Graser et al. 2012). Furthermore, in some circumstances, effect of human-driven changes varies according to sex or life stage. For example, in Silver Gulls (*Larus novaehollandiae* Stephens, 1826 = *Chroicocephalus novaehollandiae* (Stephens, 1826)), males from an urban colony were heavier than males from a remote colony, but female body mass was not affected (Auman et al. 2008). Understanding how human-driven changes affect body mass is critical because body mass is a key trait influencing survival, reproduction (Peters 1986), and population dynamics in mammals (Pelletier et al. 2007).

Our objective was to explore the relationship between human activity (human density, area with artificial food sources, edges of forested area bordering corn (*Zea mays* L.) fields) and body mass. Raccoons (*Procyon lotor* (L., 1758)) are a quintessential example of an “urban exploiter” and, therefore, a model for understanding the effects of human activity on body mass. Raccoon population density is highest in heavily human-modified landscapes, such as urban centers (Riley et al. 1998; Smith and Engeman 2002; Prange et al. 2003), and in agricultural landscapes (Beasley et al. 2011; Houle et al. 2011). Artificial food sources, such as refuse and corn, are hypothesized to explain these high raccoon densities (Riley et al. 1998; Prange et al. 2004). These food subsidies associated with anthropogenic landscapes are also thought to cause increased body mass (Rosatte et al. 1991). However, this assertion remains untested.

In this paper, we assess the effects of human activity, i.e., the effect of being near humans and being near artificial food sources on body mass. We hypothesize that human-driven landscape modifications will be critical drivers of variation in raccoon body mass. As human population density has been linked to high raccoon population density (Riley et al. 1998; Prange et al. 2004), we predict it will have a positive effect on body mass (P_{1A}). Alternatively, if higher human population density increases stress due to density dependence and conspecific competition, we predict a negative effect on body mass of raccoons (P_{1B}). Increased access to artificial food sources has been shown to affect habitat quality (Bozek et al. 2007) and, consequently, raccoon abundance (Prange et al. 2004; Houle et al. 2011). Therefore, we expect a positive relationship between raccoon body mass and access to artificial food sources (P_2). We divided food sources into two groups: crop subsidies or refuse. In agricultural landscapes, food availability, e.g., corn fields, is critical for raccoon populations to attain high densities (Beasley et al. 2011). It is also important that resources are adjacent to protective cover, such as forest patches (Beasley et al. 2011). As a result, density of forested edges bordering corn fields (km of edges/km² of corn fields) predicts raccoon abundance well (Houle et al. 2011). Corn, however, is a seasonally available resource and its effect on raccoon density is strongest when crops reach maturity (Houle et al. 2011). Therefore, we predict a positive relationship between body mass in autumn and density of forested edges bordering corn fields (P_{2A}). Furthermore, we predict a positive relationship between body mass and area of the landscape occupied by human activity that may provide artificial food sources, such as campgrounds or residential area that are sources of refuse, but different from agricultural subsidies (P_{2B}).

Weather also affects raccoon body size (Ritke and Kennedy 1988; Pitt et al. 2008). During winter, raccoons undergo dormancy and

depend almost exclusively on fat reserves gained during the previous autumn (Hoffmann 1979; Gehrt and Fritzell 1999). At the northern limit of their range, raccoons can lose up to 50% of their body mass during winter (Stuewer 1943; Mech et al. 1968). Indeed, Pitt et al. (2008) showed that springtime residual body fat decreased with the previous winter's severity. The variable with the largest effect on raccoon body size is mean annual precipitation (Ritke and Kennedy 1988). Thus, we predict that an increase in previous winter severity (P_{3A}) and in mean annual precipitation (P_{3B}) will decrease body mass.

Materials and methods

Study area and captures

Our study was conducted in southern Quebec, Canada (Supplementary Fig. S1a).¹ The landscape is dominated by an east–west agricultural intensification gradient (Ghilain and Bélisle 2008). The eastern portion of the study area is characterized by non-intensively farmed fields. These are mainly hay and pastureland, with more than half of the landscape occupied by forest and a few small towns. Conversely, >50% of the western portion of the study area is occupied by large, intensively managed agriculture fields, predominantly corn and soybean (*Glycine max* (L.) Merr.). Numerous, large urban centers are also found in the western end of the study area (Fig. S1b).¹

For 3 years (2007–2009), raccoons were live-trapped (763 males and 725 females; for details see Supplementary Table S1¹) during the raccoon rabies surveillance and control program in southern Quebec (for details see Rees et al. 2011). To control for seasonal body-mass variation, we limited our analysis to raccoons captured between 25 September and 21 October (Stuewer 1943; Pitt et al. 2008). We also included capture date in all our analyses (see below). For each animal captured, the location (using a hand-held Global Positioning System (GPS)), body mass (kg), and sex were recorded. To determine age, a premolar was extracted from each individual and cementum annuli were counted (Matson's Laboratory LLC, Missoula, Montana, USA; Matson 1981). Raccoon abundance was estimated in each trapping cell, using trapping success as a proxy. It was calculated as the number of unique raccoons captured per 100 traps × nights (for details see Rees et al. 2011; Mainguy et al. 2012).

Environmental characteristics

We performed spatial analysis using Geospatial Information System (GIS) ArcMap version 9.2 (ESRI, Inc. 2006). We calculated landscape variables in a buffer zone around each raccoon capture at three different spatial scales. According to Rees et al. (2008), mean home-range sizes for male and female raccoons are approximately 3.52 and 1.28 km², respectively. Because the capture position is not necessarily at the center of the home range, we used a radius of 1 and 2 km for each buffer, which is approximately the home-range diameter. In addition, we included a 5 km radius buffer to represent the maximum distance traveled as suggested by Rosatte et al. (2010) to be a proxy for dispersal by an individual over a 2-year period. Finally, we ensured that less than 2% of the landscape information was unknown at each spatial scale.

Human activity

We used data from the 2006 Canadian census, the closest available data to our sampling years (Statistics Canada 2007a, 2007b), to assess human population density in our study area. First, we calculated the human density in each geographic unit of the census. Then, we calculated the mean human density around each raccoon capture at the three spatial scales (i.e., 1, 2, and 5 km). We performed a cluster analysis to obtain three classes of human density

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2014-0263>.

(i.e., rural, suburban, and urban), following Prange et al. (2003). To do so, we used the *K*-means cluster analysis (R Development Core Team 2009) that separates individuals into a given number of predefined bins by minimizing the sum of squares from the centers of each group. This approach also limited the correlation between human density and human artificial food sources, allowing us to include both variables in our subsequent analyses.

We used the EcoForestry Information System (EFIS) to calculate for each spatial scale the area (km²) where human activity provided refuse, such as residential area, camping ground, or dumping ground. We calculated the proportion of corn fields within the spatial scale using the Assured Crop DataBase (ACDB) of Quebec. We combined EFIS and ACDB information and used Geospatial Modelling Environment version 0.7.1.0 (Beyer 2012) to calculate length of edges of forested area bordering corn fields (km). We then converted this variable into edge density by dividing the length of corn fields–forest border by the area of available corn fields (for details see Houle et al. 2011). For more information on maps and information used for landscape characterization see Supplementary Table S2.¹

Weather

We used the National Climate Data and Information Archive to find the nearest weather station for each raccoon capture and then calculated climatic variables. Following Pitt et al. (2008), we calculated winter severity as the sum of the number of days where the temperature was less than or equal to −15 °C and the number of days where snowfall exceeded 15 cm between 1 November and 31 March of the previous winter. This sum was then divided by 5, the number of months. We also used the Climate Normals and Averages from which we extracted the mean annual precipitation at the nearest weather station.

Statistical analyses

Age- and sex-specific patterns in body mass

To describe age-specific body-mass patterns, we compared five curves (see Supplementary Table S3)¹ to fit the body-mass age-specific regression. Raccoons in our study area exhibit sexual dimorphism in body mass (Jolicoeur et al. 2012); thus, we separated males and females in all analyses. We selected the model with the highest adjusted *R*² between predicted and observed body masses for males and females separately. Age-specific changes in body mass of raccoons were best described using an asymptotic model (Fig. 1; adjusted *R*² = 0.69 and 0.58 for males and females, respectively). We grouped all raccoons ≥7 years old into one age category because of limited sample size (*n* = 40). Based on Fig. 1, we determined that raccoon growth reached an asymptote at 2.5 years. Thus, in subsequent analyses, we used three age classes; juveniles (0.5 years), yearlings (1.5 years), and adults (2.5 years and older) for males and females.

Effects of environmental characteristics on body mass

We tested all independent variables (presented in Supplementary Table S4)¹ for correlations and collinearity. All pairs of variables had correlations <0.6 and variance inflation factors <3. Furthermore, we standardized each explanatory variable by their mean values to facilitate comparisons. We used generalized linear models (GLMs) with Gaussian error distribution to assess the relationship between raccoon body mass and environmental covariates. We evaluated in one model the influence of human activities (i.e., human density class, edge density, human activities providing food sources) and weather effects (i.e., winter severity, mean annual precipitation). We also tested for interactions between human activities and weather. We controlled for variation among sample years, Julian day, and local raccoon abundance by including these three variables as fixed effects in each candidate model. To estimate the relative contribution of environmental characteristics, we applied the method used by Pelletier et al. (2012): we

removed one covariate at a time from the full model and calculated the difference in adjusted *R*². The difference between the full model and the model without a specific environmental covariate (ΔR^2) is considered the importance of this covariate. We performed separate analyses by age class (i.e., juveniles, yearlings, and adults) and sex (i.e., females and males) and replicated across spatial scales (i.e., 1, 2, 5 km). We plotted parameter estimates of all human effects and weather variables against spatial scales to compare effect direction and size. We performed all statistical analysis using R version 2.10.0 (R Development Core Team 2009).

Results

Effects of environmental characteristics on body mass

Overall, models explained between 3% and 25% of the variance (adjusted *R*²) depending on sex, age class, and spatial scale (Table 1). For females, full models explained 10%–12% of the variance in mass for juveniles (young of the year), 16%–17% for yearlings, and 13%–16% for adults. The best model fit for juveniles, yearlings, and adults were at 2, 1, and 5 km, respectively. Winter severity was the most important environmental variable affecting female juveniles and yearlings at all spatial scales. Mean annual precipitation was the most important variable for adult females at 1 km, while the area providing artificial food sources was the most important variable at 2 and 5 km.

For males, full models explained 3%–5% of the variance for juveniles, 22%–24% for yearlings, and 12%–13% for adults. The best model fit for juveniles, yearlings, and adults occurred at 1, 5, and 1 km, respectively. Mean annual precipitation was the most important variable explaining variation in yearling mass at all spatial scales. The area providing artificial food sources was the most important variable for male juveniles at 1 and 2 km. Edge density of forested area bordering corn fields was the most important variable explaining male adult mass at 1 and 2 km. Human density class was the most important variable for adult males at 5 km.

Human activity

Human population density classes determined by *K*-means cluster analysis were 0–44 people/km² for rural, 44–448 people/km² for suburban, and >448 people/km² for urban. The effect of human density differed according to raccoon sex, age, and spatial scale (Supplementary Table S5¹ and Figs. 2a–2d). It had a significant positive effect on body mass of females only for adults at the 5 km radius zone and a negative effect on body mass of males only for juveniles at the 1 km radius zone. Human population density classes did not significantly affect other age and sex classes at any spatial scale. Landscapes where human activity provided artificial food sources (Supplementary Table S5¹ and Figs. 2e, 2f) had a negative effect on body mass of juvenile and adult females at the 2 and 5 km radius zones. Conversely, it had a positive effect on body mass of male juveniles at the 1 and 2 km radius zones. Edge density of forested area bordering corn fields (Figs. 2g, 2h) had negative effects on body mass of juvenile females at the 2 km radius zone but had a marginally positive effect on body mass of adult males at the 2 km radius zone.

Weather

Winter severity had a significant negative effect on body mass of female juveniles at all spatial scales (Supplementary Table S5¹ and Fig. 3a) and marginally significant effect on female adults at the 1 and 2 km radius zones. We found no effect of winter severity on males at any age class or spatial scale (Fig. 3b). Mean annual precipitation had a positive effect on body mass of female juveniles at the 1 and 2 km radius zones and adults at the 1 km radius zone (Fig. 3c). Mean annual precipitation affected significantly and positively body mass of male yearlings at the 1, 2, and 5 km radius zones (Fig. 3d). Most interactions between human activities and weather were not significant. In the few models where interactions were selected (5 out of 18), the interactions were driven by

Fig. 1. Age-specific body mass recorded between 25 September and 21 October of 1488 raccoons (*Procyon lotor*) captured in southern Quebec, Canada, between 2007 and 2009.

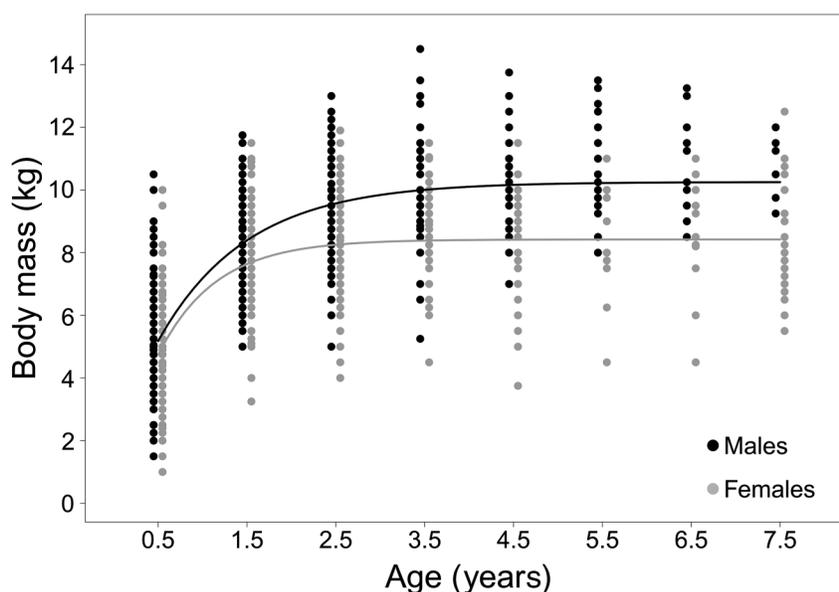


Table 1. Variance in body mass explained (adjusted R^2) by the full model and the partial variance explained by each environmental variable separately for age class and spatial scale for (a) female and (b) male raccoons (*Procyon lotor*) captured in southern Quebec, Canada, between 2007 and 2009.

	1 km			2 km			5 km		
	Juveniles	Yearlings	Adults	Juveniles	Yearlings	Adults	Juveniles	Yearlings	Adults
(a) Females									
Full model	0.102	0.174	0.135	0.122	0.16	0.148	0.121	0.165	0.164
Human density (classes)	<0.001	0.002	0.003	0.007	0.002	0.003	0.011	0.004	0.018
Edge density	0.006	0.012	0.002	0.016	0.001	<0.001	0.004	0.003	0.004
Artificial food sources	<0.001	0.006	0.002	0.012	<0.001	0.016	0.019	0.001	0.036
Winter severity	0.045	0.013	0.009	0.067	0.009	0.011	0.056	0.012	0.006
Mean annual precipitation	0.023	0.006	0.013	0.011	0.008	0.008	0.006	0.008	0.005
(b) Males									
Full model	0.054	0.229	0.136	0.041	0.243	0.135	0.03	0.246	0.127
Human density (classes)	0.013	<0.001	0.001	0.007	0.004	0.002	0.003	<0.001	0.006
Edge density	0.004	0.002	0.008	0.002	0.013	0.011	<0.001	0.014	<0.001
Artificial food sources	0.023	<0.001	0.005	0.011	<0.001	0.002	0.002	0.005	<0.001
Winter severity	<0.001	0.004	0.001	0.002	0.005	0.001	0.001	0.004	<0.001
Mean annual precipitation	0.005	0.056	0.001	0.006	0.049	<0.001	0.004	0.043	0.001

Note: The variance explained by a specific environmental variable is calculated as the difference between the adjusted R^2 of the full model and the adjusted R^2 of the model excluding the variable of interest. The most important environmental variable for a sex, age class, and scale are set in boldface type.

outliers. When these outliers were removed, however, all interactions were no longer significant; thus, we do not report them.

Discussion

In this article, we investigated the effect of urbanization and other human-driven environmental changes for a species often considered an urban exploiter. We showed that distinct life stages and sexes respond contrastingly to environmental characteristics at different spatial scales, in opposite directions, and with variable effect sizes. Many studies focused exclusively on the general impact of human activity (i.e., urbanization) and its effect on body mass (Cypher and Frost 1999; Auman et al. 2008; Graser et al. 2012). We went further by trying to disentangle the effect of being near humans and being near food sources provided by humans. We also divided these artificial food sources into refuse-type resources and agricultural food sources. We showed that human density affected body mass negatively for males but positively for females.

We also showed that artificial food sources affected body mass positively for males but negatively for females. Contrary to our expectations, however, human-driven changes explain relatively little variance in raccoon body mass.

Perhaps due to the high variability within and between sexes and age classes, our main expectation that modified landscapes were critical drivers of body mass was not supported. Because raccoons thrive in human-modified landscapes, we expected that human-driven changes would explain a large proportion of the variation in body mass. However, variance in body mass explained by human activity (i.e., the cumulative effects of human density, artificial food sources, and edge density) was lower than 6% ($\Sigma\Delta R^2$). We maintain that human-activity effects, however weak, are important factors affecting body mass. These effects might have been masked by a number of life-history and behavioral traits. For example, juveniles (the age group with the lowest variance explained)

Fig. 2. Beta (β) coefficients (and 95% confidence intervals (CI)) describing the effect size of human-activity variables (*a–d*: human population density classes; *e, f*: human activity providing artificial food sources; *g, h*: edge density of forested area bordering corn (*Zea mays*) fields) included in the complete model explaining body mass of raccoons (*Procyon lotor*) at each spatial scale. Left column denotes models with females (*a, c, e, g*) and right column denotes models with males (*b, d, f, h*). Black circles and broken lines are for juveniles; dark grey circles and dotted lines are for yearlings; light grey circles and solid lines are for adults.

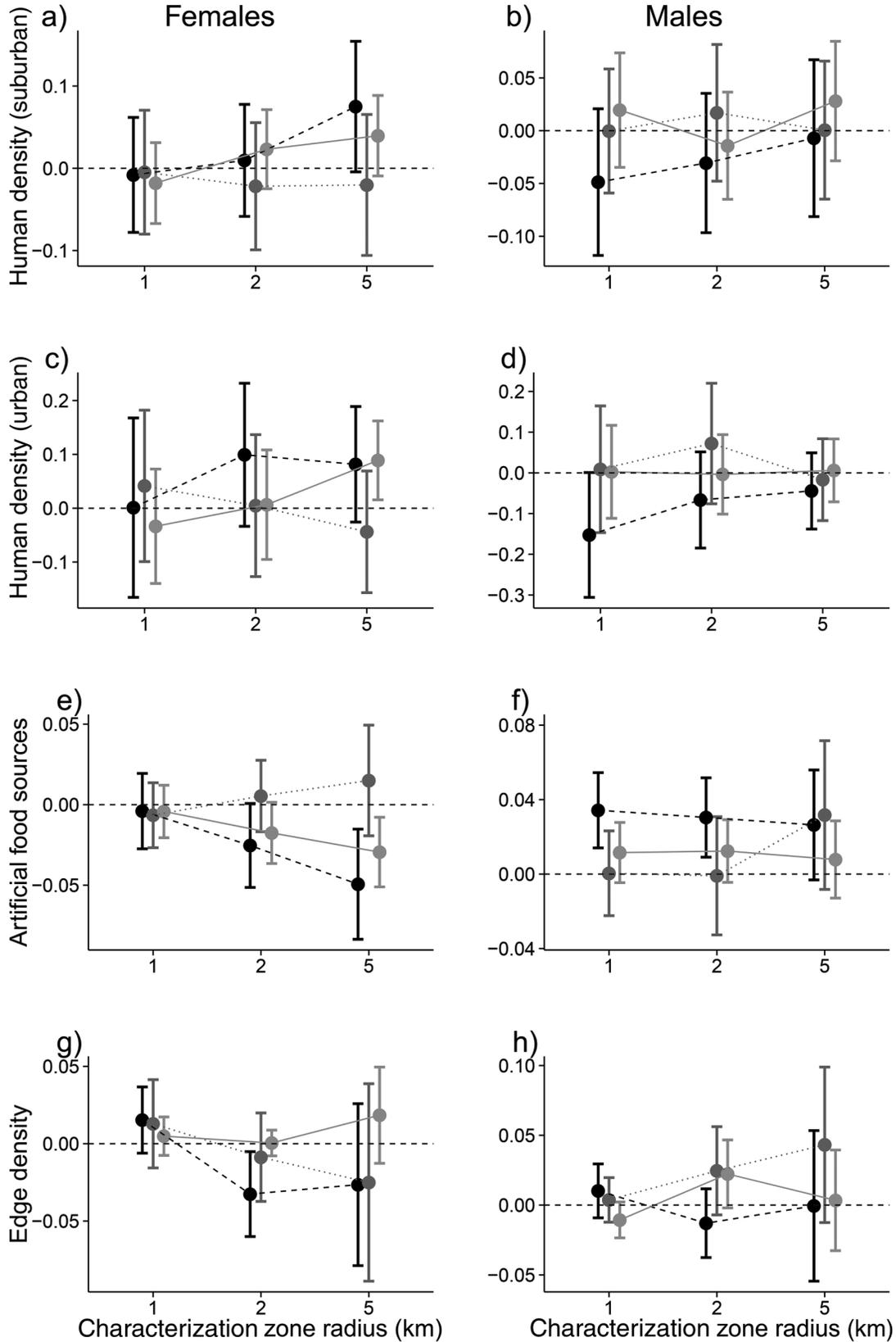
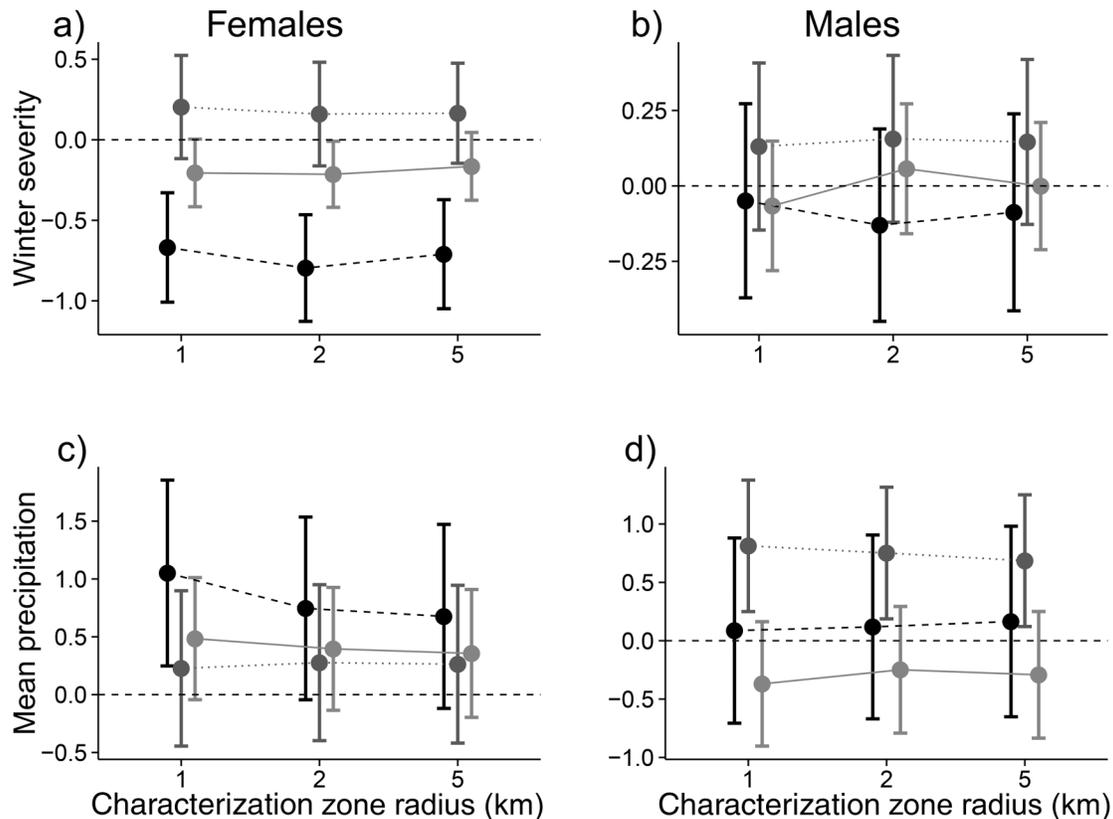


Fig. 3. Beta (β) coefficients (and 95% confidence intervals (CI)) describing the effect size of weather variables (*a, b*: winter severity; *c, d*: mean annual precipitation) included in the complete model explaining body mass of raccoons (*Procyon lotor*) at each spatial scale. Left column denotes models with females (*a, c*) and right column denotes models with males (*b, d*). Black circles and broken lines are for juveniles; dark grey circles and dotted lines are for yearlings; light grey circles and solid lines are for adults.



may be affected by maternal effects that mask other environmental effects.

Another variable that could have masked the effect of human activity on body mass is body size. Unfortunately, we could not test this because no skeletal or structural sizes were available to us. However, body mass has been shown to integrate variation in several body-condition components and some researchers suggested that information on mass should be prioritized to describe variations in body condition (Taillon et al. 2011). In raccoons, it has been shown that morphometric indices of body conditions are only poor estimators of total body fat (Pitt et al. 2006). Thus, although controlling for body size may have helped us differentiate between small fat and long lean raccoons and potentially increase the variance explained in some of our models, we suspect that it would not have changed the direction of the effects reported here.

Despite raccoons being urban exploiters, most body-mass variation in our models was explained by winter severity and precipitation, rather than by human-driven causes. These results highlight that even modified habitats cannot fully buffer against severe weather. For instance, winter severity had negative effects on body mass of females as predicted in P_{3A} . However, the effect was significant only in juveniles. Raccoons are conceived in February–March and born in April–May (Stuewer 1943; Rees et al. 2008). Therefore, winter severity may be a maternal effect. A greater effect of winter severity has been recorded in early spring, when raccoons may lose up to 50% of their fat reserves (Pitt et al. 2008). Raccoons, however, are capital breeders that accumulate mass in summer such that by autumn their percentage of body fat remains relatively invariable interannually (Pitt et al. 2008). A mother's condition during pregnancy (winter) and lactation (spring – early

summer) may explain the effect of winter severity on juvenile body mass.

Mean annual precipitation also explained more variance in our models than did human activities. In contrast to our prediction (P_{3B}) and previous research (Ritke and Kennedy 1988), precipitation had a positive effect on raccoon body mass in our system. Our results may differ from those of Ritke and Kennedy (1988) because absence of water—an important resource for raccoons (Stuewer 1943; Lotze and Anderson 1979)—has a negative effect on growth at large spatial scales (Ritke and Kennedy 1988), but may positively affect body mass at finer spatial scales. Raccoons need access to water near dens and in their home ranges (Henner et al. 2004; Bozek et al. 2007). As such, mean annual precipitation may positively influence raccoon body mass at fine spatial scales.

The effects of artificial food sources were also different in direction between the sexes. Landscapes where human activities increased access to artificial food sources, such as refuse or corn, significantly and positively affected male body mass. These results are in accordance with predictions P_{2A} and P_{2B} . Males near human activity and artificial food sources were heavier than males from populations in natural habitats. Conversely, landscapes providing artificial food sources and edge density of forested area bordering corn fields had negative effects, when significant, on female body mass. These results were contrary to our predictions (P_{2A} , P_{2B}). In previous studies, female body mass, however, were weakly correlated with artificial food sources (Beckmann and Berger 2003; Auman et al. 2008). Research involving reproductive success and population dynamics is necessary to further disentangle this conflict between the sexes.

In an increasingly modified and developed world, some species have adapted and benefited from these changes (Ditchkoff et al. 2006; Bateman and Fleming 2012). In this study, we disentangle the relative importance of environmental variables linked with human activities and weather on the body mass of an urban exploiter, the raccoon. Although artificial food sources and edge density explained more variation than human density, both failed to buffer the effect of weather. Nevertheless, increased availability of artificial resources, for those species that can exploit them, may compensate for negative effects of human density that cause high levels of stress and contribute to mortality. We also argue that individual spatial scale analysis gives a better portrait of adaptation to human-modified landscapes, because sex and age groups clearly respond differently to environmental change. Our results for raccoons suggest species that thrive in highly human-modified landscapes may show an important sexually dichotomous response to environmental change. Whereas males tend to invest surplus resources in somatic growth, which may enhance survival and mating success, females tend to invest in increased fecundity and juvenile survival, which may contribute to a change in demographic rates in anthropogenic landscapes. This demographic transition may ultimately explain the increased abundance of some urban exploiters.

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