

# No evidence of juvenile body mass affecting dispersal in male red deer

L. E. Loe<sup>1</sup>, A. Mysterud<sup>1</sup>, V. Veiberg<sup>1,2</sup> & R. Langvatn<sup>2</sup>

<sup>1</sup> Department of Biology, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway

<sup>2</sup> Norwegian Institute for Nature Research, Trondheim, Norway

## Keywords

body mass; body condition; emigration; condition dependence; ungulates; large herbivores; ruminants.

## Correspondence

Leif Egil Loe, Department of Biology, Centre for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway. Tel: +47 22 85 72 94; Fax: +47 22 85 47 26  
Email: l.e.loe@bio.uio.no

Editor: Virginia Hayssen

Received 12 March 2009; revised 20 August 2009; accepted 23 August 2009

doi:10.1111/j.1469-7998.2009.00647.x

## Introduction

Dispersal affects numerous processes in the dynamics (Rosenberry, Lancia & Conner, 1999), the persistence (Hanski & Gilpin, 1997; Clobert *et al.*, 2001; Ims & Hjermann, 2001) and the genetic structure (Bohonak, 1999) of populations. Patterns of dispersal may also influence the optimal harvesting regimes in exploited populations (Milner-Gulland, Coulson & Clutton-Brock, 2000). Despite considerable theoretical interest and importance, empirical evidence of dispersal rates and the processes determining them are scant. In spatiotemporally variable environments, *condition-dependent* dispersal (*sensu* Ims & Hjermann, 2001) occurs when individuals with a poor match between their phenotype and the external conditions disperse to find better opportunities elsewhere. Dispersal is affected by both the external environment (habitat quality, population density) and individual variability (body mass, fat reserves) (Ims & Hjermann, 2001). The pathway between an environmental condition and the dispersal response can be either direct or indirect via changes in physiology (Ims & Hjermann, 2001). Density dependence is frequently reported to affect dispersal rates (Bowler & Benton, 2005; Matthysen, 2005); but, how often the effect is mediated through changes in body condition is unclear.

Mating systems are key to understanding sexual differences in dispersal and body-condition effects on dispersal.

## Abstract

Dispersal is an important mechanism in population dynamics with a sparse empirical basis. Environmental causes of dispersal may work directly or indirectly. In a population with documented negative density-dependent male dispersal, we investigated if the effect of density on dispersal was indirectly mediated through body mass. We analysed the probability of dispersal in 170 juvenile red deer males in Snillfjord municipality, Norway, during a 20-year period of rapid population growth (1977–1997). Body mass and dispersal propensity were not related. Thus, changes in population density act directly on dispersal and are not affected by body mass. Body mass-dependent dispersal occurs in species with strong antagonistic interactions and a high cost of dispersal. Our result suggests that the cost of dispersal in male red deer is low in terms of energy expenditure and survival. We conclude that the effect of body mass on dispersal is likely to vary with mating system and cost of dispersal.

Inbreeding avoidance (Perrin & Mazalov, 1999), local resource competition (Murray, 1967; Greenwood, 1980) and/or local mate competition (Dobson, 1982) are key theoretical frameworks used to explain dispersal. Heavy, dominant individuals are expected to disperse relatively more frequently to favourable patches than smaller individuals when the transit stage is energetically costly (dispersal requires a minimum threshold of energy reserves), as occurs with ground squirrels *Spermophilus beldingi* (Nunes *et al.*, 1997). The social fence hypothesis (Hestbeck, 1982; Smith & Batzli, 2006) posits that in territorial species with strong antagonistic interactions, successful dispersal may require a large body size so that dispersers can fight off residents during a settlement phase as occurs with voles (Lambin, Aars & Piertney, 2001). In polygynous species, dispersal may be positively correlated with body size. For instance, in elephant seals *Mirounga angustirostris*, immigrant males were larger than males remaining in their natal group (Le Boeuf & Reiter, 1988). Also, in roe deer *Capreolus capreolus*, larger, sexually mature juvenile males dispersed because of increased aggression from territorial prime-aged males (Wahlström, 1994) and in white-tailed deer *Odocoileus virginianus*, yearling males with small antlers were less likely to disperse than yearlings with larger antlers (McCoy, Hewitt & Bryant, 2005). Dispersing males were reported to be larger also in red deer (Clutton-Brock, Guinness &

Albon, 1982; Clutton-Brock *et al.*, 2002), but later reports from the same population found no effect of birth mass on the probability of dispersal in any age group of males (Fan *et al.*, 2003) or females (Catchpole *et al.*, 2004). The effect of body mass on dispersal therefore deserves further attention.

Here, we investigate whether the probability of dispersal in juvenile male red deer in Norway is dependent on individual condition. We have earlier shown that the dispersal rates of males (Loe *et al.*, 2009) and body mass (Mysterud *et al.*, 2001b) were negatively related to density in this population. In the present work, we are particularly interested in determining if body mass is the mediator of the density-dependent dispersal rates of males at the individual level. More specifically, we test the following hypotheses: (H<sub>1</sub>) Dispersal is only affected by environmental condition, that is, only a direct negative effect of density (Loe *et al.*, 2009) and body mass has no effect. (H<sub>2</sub>) Dispersal is affected by individual condition in one of three ways. (H<sub>2a</sub>) The negative effect of density is mediated through a negative effect on body mass. (H<sub>2b</sub>) Additive negative effect of density and positive effect of body mass (Clutton-Brock *et al.*, 2002). (H<sub>2c</sub>) Interacting effects of density and body mass (Hanski, Peltonen & Kaski, 1991).

## Materials and methods

### Study area

The study took place in Snillfjord municipality in Sør-Trøndelag county at the west coast of Norway (63°30'N, 9°30'E). The climate is seasonal with mean January and July temperatures of -2.2 and 12.9°C, respectively. Snow cover is normally extensive in high-altitude inland areas but not along the coast in winter (December–March). The majority of female red deer seasonally migrate between coastal, lowland winter home ranges and inland summer home ranges. Each seasonal range normally covers only a few square kilometres, but the winter and summer ranges may be located up to 70 km apart (Albon & Langvatn, 1992). Relocation from winter to summer ranges normally occurs in April–May, and the return occurs in September–November. Transfer time varies from a few days up to 3 weeks. Preliminary GPS data suggest that male migratory patterns are broadly similar to females with respect to timing and distance (E. Meisingset *et al.*, unpubl. data). Median date of calving is 16 June (Loe *et al.*, 2005) and median date of ovulation (and hence mating) is 15 October (Langvatn *et al.*, 2004). Natural predation (mainly on juveniles) from red fox *Vulpes vulpes* and lynx *Lynx lynx* is limited; 85% of mortality is due to human hunting (Langvatn & Loison, 1999). The annual hunting season is from 10 September to 15 November.

### Subjects

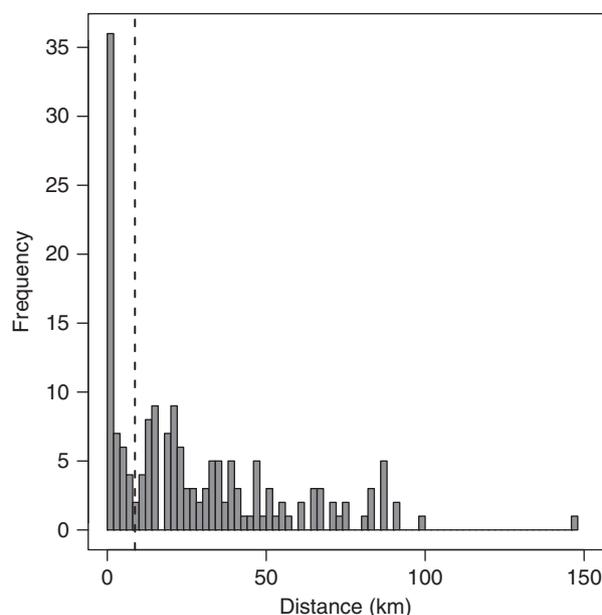
Male red deer ( $n = 170$ ) were marked and weighed as calves in their first winter (*c.* 9 months old) and recovered dead later in life (at a yearling age or older). These data are a

subset of a previous study (Loe *et al.*, 2009;  $n = 468$ ; both sexes), here restricted to male calves with known mass at marking. Marking with coloured and numbered plastic ear tags took place from 1977 to 1997 at eight different locations in Snillfjord (Albon & Langvatn, 1992). Mortality of the recovered individuals was from hunting by humans (95.7%), 'natural' causes (drowning, falling, avalanches, etc. 1.2%) and deer–vehicle collisions (3.1%).

## Statistical analysis

### Defining philopatry versus emigration

We define dispersal as being either movement from the natal area (range used by mother before weaning) to the breeding area (natal dispersal) or between breeding areas (breeding dispersal) (Clobert *et al.*, 2001). Emigration is simply the first step of the dispersal process (Ims & Hjermann, 2001; Bowler & Benton, 2005) and may not necessarily result in an individual leaving the population. We divided the recoveries into two distance categories (Fig. 1) choosing the threshold distance as the median diameter of annual 95% home ranges in seasonally migrating female red deer (8.7 km;  $n = 24$ ; unpubl. GPS data; same as in Loe *et al.*, 2009). According to this classification, 53 individuals did not emigrate (recovered <8.7 km from marking site; denoted zero) and 117 did emigrate (recovered  $\geq 8.7$  km; denoted one). This binary response variable was used in analyses of probability of emigration. We also ran analyses with dispersal distance as a



**Figure 1** Frequency of recovery distances in male red deer. The distance (km) is between the marking and recovery site. In the analyses, individuals with larger distances than 8.7 km (the dashed vertical line) are denoted as dispersers while the remaining individuals are denoted philopatric.

continuous response variable and these analyses gave qualitatively the same results (results not reported).

### Age at recovery

Age at recovery was modelled as a three-level factor variable (yearling, 2 years old and 3 years and older).

### Date of recovery

Most of the recovery data consist of harvested deer and therefore, were obtained during hunting season when migrating deer could either (1) be in their summer area; (2) be on their way back; (3) have returned to their winter area (which would be close to the marking site if the animal had not dispersed). To account for seasonal migration on the distance from the marking site, the effect of Julian date was modelled using a cyclic spline function in generalized additive models [(GAM); Woods, 2006]. A cyclic spline function was used because the predicted value is expected to be similar on Julian dates 1 and 365.

### Population density in the year of birth

The total number of red deer shot per municipality per year, divided by the area of suitable red deer habitat (as defined by the management authorities), was used as an index for local population density (Loe *et al.*, 2009). Although dispersal most frequently occurs at 1–2 years (Loe *et al.*, 2009), we chose to use the density estimate from the marking site in the year of birth, because some individuals may already have dispersed in later years. Density at the marking place varied with time. The correlation coefficient was 95% with a delay of 1 year and 87% with a delay of 2 years. The analyses are therefore rather insensitive to the choice of year of density. Regardless of the time lag of the density estimate used (0, 1 or 2 year), the parameter estimate is always negative.

### Residual body mass

Body mass at the time of marking (late winter when the calf is *c.* 9 months old) was dependent on the date of marking (as

calves lose mass during winter). Body mass was therefore included in the model below as the residual value from a linear regression of body mass and marking date (McCullagh & Nelder, 1989). In the ungulate literature, juvenile mass has a strong impact on adult mass or on fitness traits mediated through body mass (for red deer: Albon, Clutton-Brock & Guinness, 1987, for roe deer: Pettorelli *et al.*, 2002; general: Sæther, 1997; Lindström, 1999; Gaillard *et al.*, 2000). Hence, body mass at age 9 months is likely to correlate with body mass at time of dispersal.

### NAO<sub>utero</sub>

As an index of global winter climate, we used the station-based winter (December–March) index of the North Atlantic Oscillation (NAO) (Hurrell, 1995), which is known to have a strong impact on the life history of red deer along the south-west coast of Norway (Mysterud *et al.*, 2001a; Pettorelli *et al.*, 2005). We used the NAO value from the year the calf was in utero in the presented models (similar to Loe *et al.*, 2009). We also tested effects of NAO in the first and second year of life but as they had no effect on dispersal results they are not presented.

### Evaluation of competing hypotheses

Statistical models representing hypotheses H<sub>1</sub> and H<sub>2a–c</sub> (Table 1) were fitted using GAM with a logistic link and binomial error distribution (Woods, 2006). The response variable was Emigration (one or zero). Predictor variables in all four models included Age at recovery and NAO<sub>utero</sub>. The remaining predictor variables varied among models (Table 1) and included Density<sub>birth</sub>, Body Mass<sub>residual</sub> and the two-way interaction between Density and Body Mass<sub>residual</sub>. The effect of Julian Date of recovery was fitted with a cyclic spline function. All GAM were run using the library *mgcv* version 1.3-29 in R version 2.7.0 (R Development Core Team, 2008).

The model containing only density (H<sub>1</sub>; Loe *et al.*, 2009) was refitted on the smaller data set containing only males of known body mass at marking ( $n = 170$  instead of  $n = 468$  in Loe *et al.*, 2009). The AIC criterion (Burnham & Anderson,

**Table 1** Model selection of the four competing hypotheses for dispersal of Norwegian male red deer; H<sub>1</sub> only direct effect from density, H<sub>2a</sub> the effect of density works through body mass, H<sub>2b</sub> there is an additive of density and body mass, or H<sub>2c</sub> if there is an interaction between density and body mass

Hypothesis	Model	AIC	ΔAIC	AIC <sub>weight</sub>
H <sub>1</sub>	Sex + Density <sub>birth</sub> + Age dead + NAO <sub>utero</sub> + Spline (Julian date of recovery)	178.8	0	0.564
H <sub>2a</sub>	Body mass <sub>residual</sub> + Age dead + NAO <sub>utero</sub> + Spline (Julian date of recovery)	180.7	1.94	0.214
H <sub>2b</sub>	Body mass <sub>residual</sub> + Density <sub>birth</sub> + Age dead + NAO <sub>utero</sub> + Spline (Julian date of recovery)	180.6	1.87	0.222
H <sub>2c</sub>	Body mass <sub>residual</sub> + Density <sub>birth</sub> + Age dead + NAO <sub>utero</sub> + Spline (Julian date of recovery) + Body mass <sub>residual</sub> × Density <sub>birth</sub>	180.4	1.60	0.254

The most parsimonious model has the lowest AIC value and the AIC<sub>weights</sub> provide the proportional support to each model.

1998) was used to evaluate the four competing hypotheses ( $H_1$ – $H_{2a-c}$ ; Table 1).

## Results

We earlier reported that dispersal in male red deer was negatively density dependent (Loe *et al.*, 2009). In this smaller dataset, the negative effect of density is of similar strength but no longer significant (supporting information Table S1). The three models with body mass had higher AIC values and lower AIC<sub>weights</sub> than the model with only population density (Table 1). The negative effect of population density does, therefore, seem to work directly on the dispersal propensity ( $H_1$ ; Table S1; Loe *et al.*, 2009) and not indirectly through alterations of body mass ( $H_{2a}$ ; Table 2), in addition to body mass ( $H_{2b}$ ; Table S2) or in interaction with body mass ( $H_{2c}$ ; Table S3). Also, the parameter estimate of body mass is near zero (Fig. 2; Table 2) emphasizing that juvenile body mass is not affecting dispersal in male red deer.

## Discussion

We found no effect of body mass on the propensity to disperse in male red deer, although both dispersal rate and body mass were earlier reported to be negatively density dependent. Thus, dispersal was determined directly by the environmental condition (supporting  $H_1$ ) and not affected by body mass (rejecting  $H_{2a-c}$ ). The direct effect of density may arise if individuals use encounter rate of potential mates and competitors as well as amount of food as cues for dispersal (Loe *et al.*, 2009). Reasons for the lack of body mass effect on dispersal could be a combination of the following (1) low costs of exploration and dispersal in terms of energy expenditure or mortality during these movements (low-cost transfer stage); (2) limited antagonistic interactions during emigration in early summer (no eviction from natal range and easy settlement in new range). Throughout the study period, the number of deer around the marking localities increased (Loe *et al.*, 2009). In the beginning of the study period, even short-ranging individuals may have discovered and dispersed to areas of better foraging condi-

tions, as low-density areas were close to the marking site. At the end of the study, only far-ranging individuals may have found better foraging areas in low-density areas now only available far from the marking site. Consequently, if a large individual variation exists in the degree of exploration behaviour, which is independent of body mass and if all males, irrespective of initial body mass, select areas with the best foraging conditions within their explored range, then dispersal in male red deer may be negatively density dependent but not affected by body mass.

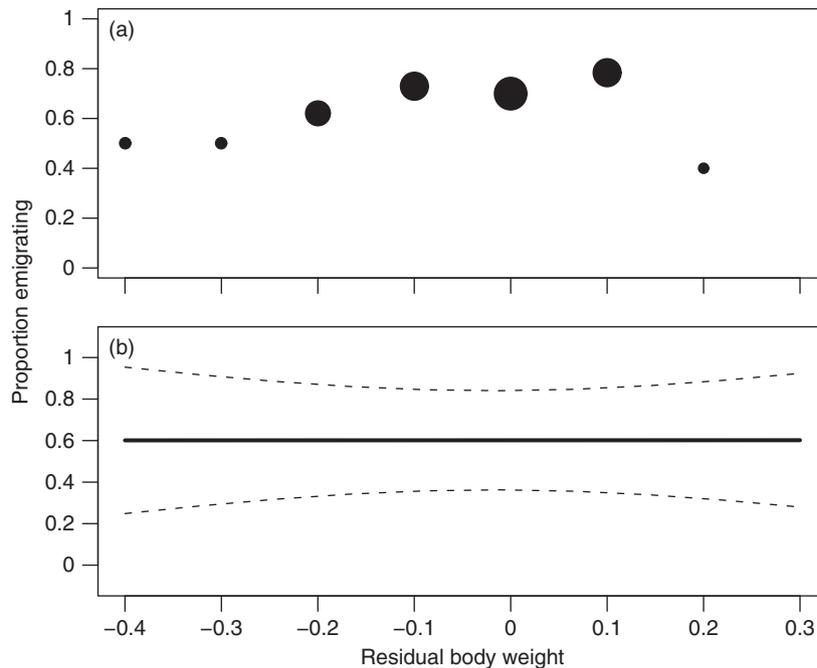
In ungulates, negative density dependence is often reported for reproduction, in particular for age at first reproduction and juvenile survival (Bonenfant *et al.*, 2009). Such density effects are almost exclusively mediated through a negative effect of body mass (Thomas, 1982; Reimers, 1983; Skogland, 1985; Langvatn *et al.*, 2004). For dispersal, the pattern is much more complex. Males are most often the dispersing sex in ungulates (Greenwood, 1980), but signs of density dependency in dispersal differ among studies from positive (Clutton-Brock *et al.*, 2002), through no effect (Nelson & Mech, 1992; Loison, Jullien & Menaut, 1999; Long *et al.*, 2005; Gaillard *et al.*, 2008), to negative (Nixon *et al.*, 2007; Loe *et al.*, 2009). Our study highlights that even when a negative effect of density on dispersal rate exists, it is not necessarily mediated through changes in juvenile body mass. Thus, the dispersal decision may be cued through mate availability and/or by a direct assessment of food quality in a similar way as any other movement event used in searching for forage (Ims, 1995).

Dispersal that depends on individual characteristics occurs commonly in insects, lizards and small mammals for which the dispersal literature is more abundant (Clobert *et al.*, 2001). Polygynous ungulates such as red deer differ from these groups many respects and these differences may explain the lack of strong evidence for dispersal based on individual phenotype. Similar to our study, lack of phenotype-dependent dispersal was reported for red deer on Rhum, Scotland (Fan *et al.*, 2003). As this population faces very different environmental conditions than the Norwegian red deer, our findings suggest that lack of phenotype-dependent dispersal may be a general pattern in red deer.

**Table 2** A generalized additive model modelling the probability of emigrating from the natal range (defined as recovery  $\geq 8.7$  km from marking site) in Norwegian male red deer ( $n=170$ )

Parametric coefficients	Estimate	SE	Z-value	P-value
Intercept	1.13	0.375	3.02	0.00255
Residual body mass	0.00461	1.42	0.00300	0.997
Age dead (yearling–adult)	0.00238	0.445	0.00500	0.996
Age dead (2 years–adult)	0.997	0.515	1.94	0.0528
NAO <sub>utero</sub>	–0.211	0.115	–1.83	0.0671
Approximate significance of smooth terms	Estimated d.f.	Estimated rank	$\chi^2$	P-value
Julian date of recovery	1.60	2	18.3	<0.001

Denoted by the insignificant parameter estimates, emigration is not a function of residual body mass. The reference level for the effect of age class is 'Adult'.  $R^2=0.229$ .



**Figure 2** Probability of emigrating (defined as recovery  $\geq 8.7$  km from marking site) in male red deer in Snillfjord municipality, as a function of residual body mass (corrected for marking date). (a) This panel shows the raw data. Point estimates (circles) are the proportion of emigrants in residual body mass classes (the area of the circles being proportional to sample size). (b) Predicted values of the probability of emigrating with increasing residual body mass after accounting for other factors (see the model in Table 1;  $H_{2a}$ ). The date for the prediction is set to 1 November, when most seasonal migrants will have returned to their winter site and within the time period were we have most data.

For the great majority of polygynous male ungulates, frequency and severity of antagonistic interactions are limited to the short rutting season, which generally occurs during fall. These interactions are linked to female defence rather than spatial territories, and they are unlikely drivers for emigration and immigration that occurs mainly in early summer. An exception is roe deer that defend a mating territory for most of the growing season, and for which larger and sexually mature juvenile males are more likely to get evicted by dominant males (Wahlström, 1994). In white-tailed deer, distinct seasonal cues are important proximate causes of dispersal, and only fall, not spring, emigration increased with increased competition among males (Long *et al.*, 2008). Many large herbivore populations, such as the red deer in our study, occupy areas of continuous habitat cover where migration corridors often consist of the normal feeding habitat. Young individuals show exploratory behaviour before dispersing (Van Moorter *et al.*, 2008) and the energy cost of exploration and subsequent dispersal may be relatively small and affordable even for low-quality individuals. For populations with very low rates of natural predation, large variation in survival between philopatric and dispersing individuals is not expected (snow shoe hares *Lepus americanus*; Gillis & Krebs, 2000). Low energetic costs of dispersing as well as the lack of any substantial difference in predation probability in familiar and unfamiliar areas may be causal factors explaining the lack of effect of individual body condition in our study.

Although the negative density-dependent dispersal was not mediated through body mass, we cannot exclude other indirect pathways. Sex hormones predispose natal dispersal in a range of species (Dufty & Belthoff, 2001). In male European badgers *Meles meles*, natal dispersal correlated positively with the level of testosterone (Woodroffe, Macdonald & Dasilva, 1995) and neonatal female ground squirrels treated with testosterone displayed male-like dispersal patterns as juveniles (Holekamp *et al.*, 1984). The role of testosterone in male ungulate dispersal is not known.

Increasing population density has a delayed negative effect on body mass through herbivory-driven changes to the plant community (Myserud *et al.*, 2002; Simard *et al.*, 2008). Decreasing body mass further translates into reduced juvenile survival and delayed age at first reproduction. Our results provide evidence that the density effect on dispersal is more direct than observed for other vital rates. Body mass is not an important determinant of dispersal in red deer. Thus, we predict that the cost of dispersal in ungulates is low. Novel insight may also be gained through telemetry data from juveniles in order to investigate individual variation in exploratory behaviour early in life and if the degree of exploration influences the probability of dispersal.

## Acknowledgements

These analyses were made possible by grants from the Research Council of Norway (YFF project 163061 and the

AREAL-project 179370/I10). Thanks to Virginia Hayssen, Jean-Michel Gaillard and one anonymous referee for very valuable comments.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** A generalised additive model (GAM) modelling the probability of emigrating from the natal range as a function of density at marking site in the year of birth (hypothesis H<sub>1</sub>) and controlled for the effect of other variables. This is a similar model to the one presented in Loe *et al.* 2009 (see text above for a comparison of the models). The reference level for the effect of age class is 'Adult'.  $R^2 = 0.248$ .

**Table S2.** A generalised additive model (GAM) modelling the probability of emigrating from the natal range as a function of density at marking site in the year of birth and residual body mass at time of marking (additive effects; hypothesis H<sub>2b</sub>) and controlled for the effect of other variables. The reference level for the effect of age class is “Adult”.  $R^2 = 0.244$ .

**Table S3.** A generalised additive model (GAM) modelling the probability of emigrating from the natal range as a function of density at marking site in the year of birth, residual body mass at time of marking and the interaction

between them (hypothesis H<sub>2c</sub>) and controlled for the effect of other variables. The reference level for the effect of age class is “Adult”.  $R^2 = 0.248$ .

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