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10  **Long Term Trends and Correlates of Antler Anomalies in Roe Deer**

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17  **ABSTRACT** Length and structural complexity of antlers provide an indication of

18  individual quality in many ungulates in the context of female mate choice and trophy

19  hunting. Selectivity of hunters for individuals with various antler sizes may have bearing

20  on the population structure. It is less well understood, however, whether and how antler

21  anomalies may signal individual characteristics. We used data on 2,461 roe deer

22  (*Capreolus capreolus*) males harvested by stalking during 1966–2011 in western Poland

23  to test hypotheses explaining probability of occurrence of accessory, broken, and

24  malformed antlers. By employing a multinomial logistic regression, we showed that the

25  probability of occurrence of broken and malformed antlers increased in males older than

26  2 years. Probability of occurrence of accessory and, in young males, broken antlers was

27  higher in individuals with increased body weight. Occurrence of malformed antlers

28	decreased over the study period. Contrary to our prediction, we did not detect an effect of

29	distance to forest on the probability of malformed antlers occurring. We conclude that the

30	main premise of compensatory culling is not supported in roe deer.

31	**KEY WORDS**: Age, antler, body mass, *Capreolus capreolus*, habitat gradient, harvest,

32	malformation, trend, trophy.

33	Antlers of most *Cervidae* are believed to have developed primarily as signals for female

34	mate choice (Clutton-Brock 1982, Bubenik 1990*a*). The signaling function of antlers has

35	been supported by showing positive correlation between conspicuous traits of antlers,

36	such as size (i.e., length and mass) and structural complexity and some fitness surrogates.

37	Examples include correlation with lifetime reproductive output, sperm quality, and social

38	status in red deer (*Cervus elaphus*; Bartoš et al. 1988, Kruuk et al. 2002, Malo et al.

39	2005), body mass and immunological capacity in white-tailed deer (*Odocoileus*

40	*virginianus*; Harmel et al. 1989, Ditchkoff et al. 2001*a*), body mass in moose (*Alces*

41	*alces*; Solberg and Sæther 1994), and body mass and territorial status in roe deer

42	(*Capreolus capreolus*; Pélabon and van Breukelen 1998, Hoem et al. 2007, Vanpé et al.

43	2007).

44	Signaling function of antlers has also been scrutinized in the case of more subtle

45	structural characteristics, referred to as fluctuating and directional asymmetry. The

46	former and latter have been defined as small random and systematic differences,

47	respectively, in the shape between right and left antler. Fluctuating asymmetry may

48	reflect aspects of individual quality in some populations (e.g., Folstad et al. 1996,

49	Pélabon and van Breukelen 1998, Bowyer et al. 2001, Ditchkoff et al. 2001*b*, Mateos et

50 al. 2008) but not all (Kruuk et al. 2003, Bartoš et al. 2007). Directional asymmetry does

51 not serve as such a signal.

52       Less effort has been devoted to studying potential signaling function of antler

53 anomalies, such as accessory, broken, or malformed antlers. These conspicuous features

54 may provide signals for aspects of interspecific interaction such as mate choice or

55 territory establishment. For example, accessory antlers result from repeated injury of

56 tissue from which pedicles grow and are regrown and cast repeatedly once induced

57 (Bubenik and Hundertmark 2002). Formation of malformed antlers may also reflect

58 senescence as it is potentially affected by hormonal imbalance (Bubenik 1990*a*, von

59 Ueckermann 1995, Carrasco et al. 1997, Kierdorf and Kierdorf 2002). Malformed antlers

60 may also signal sensitivity to Staphylococcal infection (Gal et al. 2011), and/or

61 inflammation (Topiński 1975). In addition, some other factors have also been suggested

62 to cause antler malformation such as pedicle amputation or excess of retinol derivative

63 retinoic acid (Kierdorf and Kierdorf 2011).

64       Our understanding of factors that control shape of antlers and occurrence of antler

65 anomalies in natural populations is still limited (Kierdorf and Kierdorf 2011). In this

66 study, we describe occurrence of accessory, broken, and malformed antlers in a

67 population of roe deer males harvested in western Poland. We test the following 3

68 hypotheses on the correlates of occurrence of these antler anomalies:

69       1. Probability of occurrence of accessory antlers is higher in older than younger

70         males. This prediction stems from the fact that the risk of repeated injury

71         increases with time. Roe deer is among the species particularly responsive to

72         develop accessory antlers (Bubenik 1990*b*).

73    2. Risk of antler breakage, which is primarily caused by severe injury, is random

74    in respect to age. Hence, we test the prediction that probability of occurrence of

75    broken antlers does not differ between young and old males.

76    3. Probability of occurrence of malformed antlers is nonrandom in respect to age,

77    body mass, and habitat. We test the prediction that the occurrence of malformed

78    antlers is higher in older and/or lighter inferior males and in individuals harvested

79    at shorter distance from the forest. A series of studies from France have shown

80    that a higher quantity and/or quality of resources for roe deer may occur in open

81    agricultural habitat compared to forest, particularly so during the period of antler

82    growth in winter (Hewison et al. 2009; Abbas et al. 2011, 2013).

83 **STUDY AREA**

84 We obtained data from the experimental area of the Polish Hunting Association Research

85 Station at Czempiń, Poland (52°08' N, 16°44' E; Mysterud et al. 2006). This is an

86 agricultural landscape of approximately 150 km$^2$ with a dense network of field roads,

87 drainage ditches, and other landmarks. Eighty percent of the area is agricultural. The rest

88 is covered by forest and human settlements. Roe deer inhabit mainly fields and

89 periodically use woodlot patches for resting, but parts of the local population live in small

90 forests up to 300 ha (Kałuziński 1982*a*, Pielowski and Bresiński 1982). Diet consists

91 predominantly of crop plants, mainly cereals, oil-seed rape, and grasses (about 75% of

92 the annual diet; Kałuziński 1982*b*).

93 **METHODS**

94 **Study Species and Hunting Data**

95    Roe deer are a small (approx. 20–30 kg) ruminant with rut season in July–August

96    (Andersen et al. 1998). Antlers of adult males are cast in November when their

97    testosterone levels are lowest. Immediate winter growth of new antlers follows and

98    mineralization is typically completed in February and March (Pielowski 1988, Sempéré

99    2001).

100         At the study site, hunting was allowed from 21 May to 20 October until 1975 and

101   from 11 May to 30 September afterwards. Hunting license and separate permission is

102   required to harvest each individual in a given area and time period. The hunting is

103   regulated by Polish law and is executed by the Polish Hunting Association and local

104   forest offices.

105         Roe deer bucks were killed by hobby hunters primarily for trophy hunting.

106   Foreign guest hunters were restricted to hunt in the company of local game managers. All

107   harvested animals were brought by the managers to the Research Station to prepare

108   carcasses, classify trophies, and determine age.  At the Station, a group of the same 3

109   wildlife biologists across the entire period classified trophies into 4 groups: accessory

110   (presence of supernumerary beams), broken (beam breakage), malformed (stunted and/or

111   curved antlers), or normal antlers (Pielowski 1988; Fig. 1).

112         The same crew supervised estimation of age of harvested deer according to tooth

113   replacement and wear based on a reference collection of known age mandibles for

114   standardization (Pielowski 1988). Males were accurately aged by this method up to 13–

115   15 months with confidence, but the precision decreases rapidly in males older than 2

116   years (i.e., 25–36 months old; Hewison et al. 1999, Høye 2006, Mysterud and Østbye

117   2006). Hence, we defined 2 age classes as young (<36 months old) and old (>36 months

118    old) following Hewison et al. (2009) and Pélabon and van Breukelen (1998). Carcass

119    mass was defined as live weight minus head, viscera (intestines, stomach, liver, heart, and

120    lungs), and clotted blood. It was measured to the closest 1.0 kg during the hunting period

121    of 1966–1973 and to closest 0.1 kg during 1974–2011. Game managers visually

122    estimated distance of a kill site to the nearest forest edge in the field to the nearest 10 m

123    (for distance < 100 m) or measured the distance to the nearest 100 m by plotting the kill

124    site on a scale 1:25,000 map.

125          We used data on 2,461 bucks classified by the 4 antler types that were harvested

126    during the official hunting seasons of the period 1966–2011. Data on carcass mass were

127    available for a subset of $n = 2{,}428$ bucks, and data on Euclidean distance to forest edge

128    were available for a subset of $n = 2{,}426$ bucks. Data on age category, body mass, and

129    distance to forest were available for $n = 2{,}400$ bucks.

130    **Statistical Analysis**

131    We used multinomial log-linear models to determine the influence of explanatory

132    variables on antler type with normal antlers as the reference category (Stroup 2013). We

133    included age category (young vs. old) and hunter type (local vs. foreign) as categorical

134    variables, and carcass mass, distance of kill site to forest, and year as continuous

135    variables. We included effect of hunter type as a covariate to control for known

136    differences in trophy selectivity between local and foreign hunters in our study area

137    (Mysterud et al. 2006). We considered effect of year to check for long-term trends in

138    occurrence of anomalies. We adopted a forward model selection strategy to reach the

139    final model for inference. We started with the null model (intercept only) and used the

140    likelihood ratio test based on $\chi^2$ distribution to test whether inclusion of any of the

141    explanatory variables, 1 by 1 (up to 2-way interactions), was supported in the final

142    model. Package effects for R was used to graphically represent the model terms (Fox and

143    Hong 2009).

144    **RESULTS**

145    Accessory antlers and broken antlers typically occurred on only 1 side of the skull,

146    whereas malformed antlers most often grew on both sides (Table 1). Proportion of antlers

147    with anomalies among harvested bucks ranged from 0.65% for accessory antlers to

148    4.96% for malformed antlers (Table 1).

149    The model including the effect of age category was supported over the model

150    including only the intercept (likelihood ratio test: $\chi_3^2 = 29.1$, $P \leq 0.001$).  The effects of

151    carcass mass ($\chi_3^2 = 22.9$, $P \leq 0.001$) and year ($\chi_3^2 = 10.2$, $P = 0.02$) were also supported.

152    The effects of distance to forest ($\chi_3^2 = 6.2$, $P = 0.10$) and hunter category ($\chi_3^2 = 6.1$, $P =$

153    0.11) were not supported. The interactive term was supported over the additive effect of

154    age category and carcass mass ($\chi_3^2 = 7.3$, $P = 0.06$). The final model included the

155    interactive effects of age category and carcass mass and the additive effect of year.

156    The relative risk of growing an accessory antler increased by 1.65 for each 1-kg

157    increase in carcass mass ($Z = 2.22$, $P = 0.03$; Fig. 2). We did not detect an effect of age

158    category ($Z = 1.16$, $P = 0.25$) or year ($Z = -0.40$, $P = 0.69$) on the probability of a

159    harvested deer having accessory antlers, and we did not find an interaction between age

160    category and carcass mass ($Z = -1.22$, $P = 0.22$).

161    Probability of occurrence of broken antlers in a harvested deer was about twice as

162    high in old compared to young males ($Z = 2.32$, $P = 0.02$; Fig. 3). The relative risk ratio

163    of having broken antlers for younger males was 1.44, whereas it was 0.82 for older males

164   for a 1-kg increase in body mass ($Z = -2.21$, $P = 0.03$; Fig. 3). We did not detect an effect

165   of year on the occurrence of broken antlers among harvested males ($Z = 0.63$, $P = 0.53$).

166       Probability of occurrence of malformed antlers was about 4 times higher in old

167   than young males ($Z = 1.82$, $P = 0.07$; Fig. 4a) and decreased over the years from about

168   0.072 in 1970 to about 0.024 in 2010 ($Z = -3.22$, $P = 0.001$; Fig. 4b). We did not detect

169   any effects of carcass mass ($Z = -0.69$, $P = 0.49$) or an interaction between age category

170   and carcass mass ($Z = -0.86$, $P = 0.39$).

171   **DISCUSSION**

172   Antler development is driven by a complex neuro-hormonal regulation (Bubenik and

173   Bubenik 1990). Genetic foundation for development of antler size and structure has been

174   proved by demonstrating association between some allozyme genotypes and antler size in

175   roe deer (Hartl et al. 1998) and heritability of antler size and structure in red deer (Kruuk

176   et al. 2002) and white-tailed deer (Harmel et al. 1989, Williams et al. 1994, Lukefahr and

177   Jacobson 1998). In white-tailed deer, males with a higher level of heterozygosity had

178   larger antlers (Scribner and Smith 1990). Carrasco et al. (1997) hypothesized that antler

179   malformation found in a captive red deer male had genetic origin. However, neither

180   inbreeding nor heritability were correlated with antler deformities in a study on elk

181   (*Cervus elaphus nelsoni*) from Arizona (Hicks and Rachlow 2006). We rejected the

182   hypothesis that occurrence of malformed and broken antlers is random in respect to age

183   category, although we could not reject this hypothesis for accessory antlers.

184       Some other underlying factor correlated with age, rather than age itself, is likely

185   responsible for formation of malformed antlers.  Higher probability of malformed antlers

186   in males older than 2 years may be related to hormonal imbalance, a possible cause of

187 antler malformations (Bubenik and Bubenik 1990). Major limitation of our study in

188 identifying senescence as a main driver of hormonal imbalance lies in the inability to

189 reliably separate prime-aged males from truly senescent ones. Alternatively, reproductive

190 activity may affect hormonal balance. Higher levels of free cortisol in reproductively

191 active males compared to reproductively inactive males have been shown in other

192 mammals (e.g., Arctic ground squirrel [*Spermophilus parryii*]; Boonstra 2005). In roe

193 deer, only males older than 2 years engage in male-male competition (Hoem et al. 2007).

194 In addition, we found no evidence indicating a lower occurrence of malformed antlers in

195 larger bucks in better condition, which are expected to cope better with inflammations

196 and infections.

197     The hypothesis that antler injury happens randomly with respect to age was

198 rejected for broken antlers but not for accessory antlers. The hypothesis that occurrence

199 of accessory and broken antlers is random in respect to carcass mass was rejected for

200 both of these anomalies. The most likely explanation of these above observations is that

201 larger antlers are at higher risk of mechanical injury. Antler size correlates positively with

202 age and body mass in roe deer (Pélabon and van Breukelen 1998, Vanpé et al. 2007).

203 Superior males engage more often in contact fighting by antler wrestling (Wahlström

204 1994, Hoem et al. 2007). In old males, the relationship between occurrence of broken

205 antlers and carcass mass tended to be negative. This may be explained by increased

206 chance of antler injury in smaller and weaker males. Other sources of antler injury, (e.g.,

207 breaking antlers by accidental entangling in a wire fence) may also be responsible for

208 some of the injury-caused anomalies. Less serious injury of antlers in velvet may result in

209 development of antler malformation rather than broken antlers.

210  Surprisingly, we found no effect of location of kill site to forest distance on the

211  occurrence of malformed antlers. Investment in the development of higher quality antlers

212  has been shown to depend on diet not only in roe deer, but also in white-tailed deer

213  (Harmel et al. 1989, Vanpé et al. 2007, Lehoczki et al. 2011). Sufficient supplies of

214  nutrients and micronutrients are required for antler development (Brown 1990, Lehoczki

215  et al. 2011). The single point, kill site, likely did not sufficiently reflect spatial variation

216  in resource quantity and quality of the individual's home range. Also, the location of

217  harvest is not likely representative of habitat use during winter (i.e., in the period of antler

218  development) because of individual movements and high habitat patchiness at our study

219  site. It would be of major interest to further elucidate the physiological mechanisms

220  behind development of anomalies in antler shape.

221  Local and foreign hunters may have different preferences for antler trophies at our

222  study site (Mysterud et al. 2006). However, we did not detect any effect of hunter type on

223  occurrence of antler anomalies among harvested males. In addition, both local and

224  foreign guest hunters harvested bucks with antler anomalies in all years of the study.

225  Distinguishing between just 2 hunter categories may not capture all aspects of spatio-

226  temporal variation in hunting activity. Foreign guest hunters seek out both normal and

227  anomalous antler trophies and are dependent on the guidance provided by game managers

228  with local knowledge.  The decrease over the years in total number of game managers at

229  our study site may have resulted in worsening of their local knowledge on the spatial

230  occurrence of interesting trophy bucks. However, it cannot be excluded that decrease in

231  occurrence of malformed antlers among harvested individuals in fact reflects true

232  population processes.

## MANAGEMENT IMPLICATIONS

Antler anomalies may be a desired trophy for hunters and as such may be exposed to artificial selection. Compensatory culling has been suggested as a possible way towards sustainable trophy hunting (Mysterud and Bischof 2010). The important premise of such a practice is that by removing males with poor or anomalous antlers one removes males of lower quality. Our study does not provide evidence to support this assumption. To the contrary, we provide evidence that occurrence of accessory and broken antlers increases in heavier males. In the roe deer, body mass provides a strong cue on phenotypic quality as it is positively related to longevity and survival (Gaillard et al. 1997, 2000), probability of weaning (Hamel et al. 2009), and fecundity (Hewison 1996, Hewison and Gaillard 2001). Despite the fact that we were unable to link senescence with the occurrence of malformed antlers, it is apparent that removing a male with malformed antlers would (most often) mean removing a male in reproductive age. As a result, we argue that bucks with antler anomalies cannot be generally assumed of lower quality.

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411

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413    *Associate Editor: David Euler.*

Figure Captions



a

accessory

b

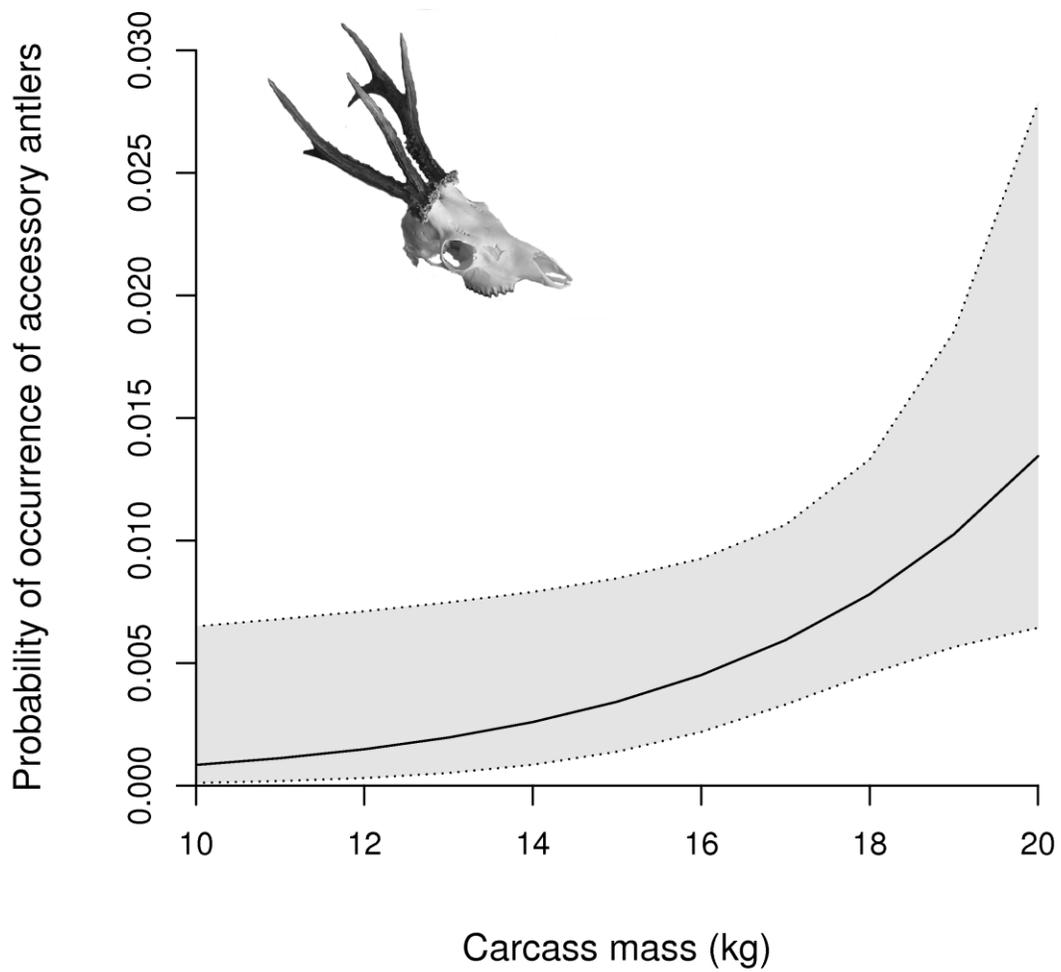broken

c

malformed

d
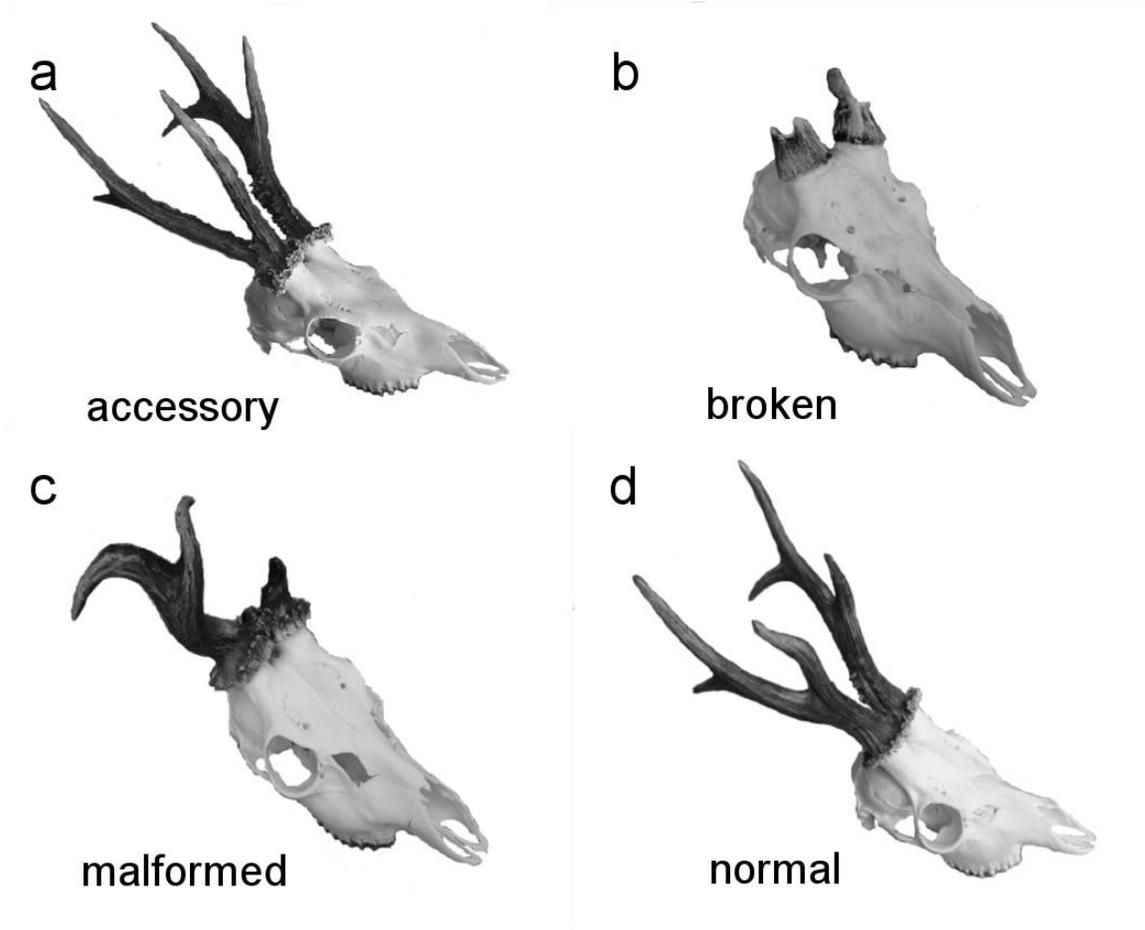
normal

416

417     Figure 1. Examples of typical a) accessory, b) broken, c) malformed, and d) normal

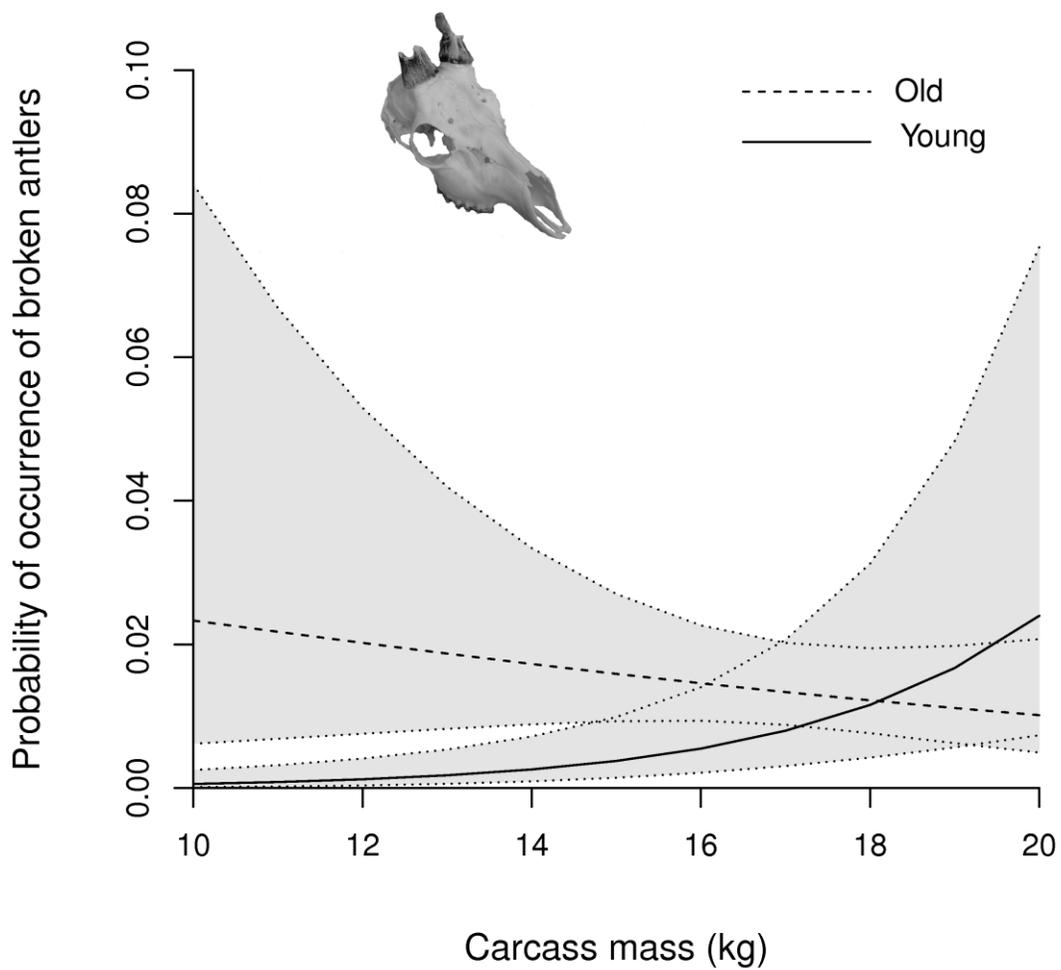418     antlers of roe deer males from western Poland.

419

420

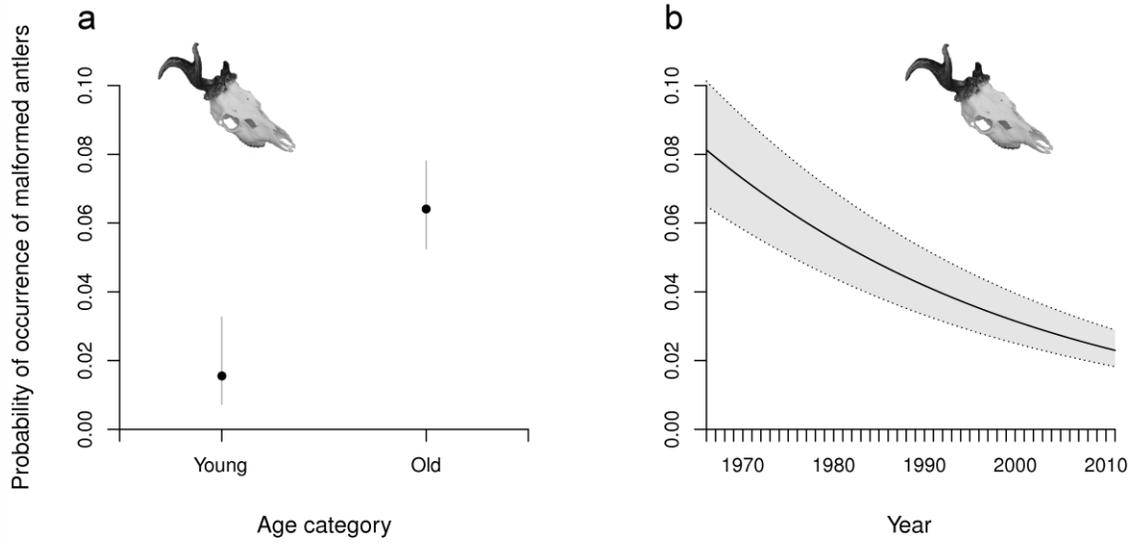421    Figure 2. Effect (with 95% CI) of carcass mass on the probability of occurrence of

422    accessory antlers in roe deer males in western Poland from 1966 to 2011.

Figure 3. Effect (with 95% CI) of carcass mass on the probability of occurrence of broken

antlers in young and old roe deer males in western Poland from 1966 to 2011.

426

Figure 4. Effect (with 95% CI) of a) age and b) year on the probability of occurrence of

malformed antlers in roe deer males in western Poland from 1966 to 2011.

429

430 Table 1. Frequency of antler anomalies in the sample of 2,461 harvested male roe deer

431 from Czempiń, western Poland, 1966–2011. The following 3 males are not included in

432 the table: 1 buck had only a single antler pedicle; 2 bucks had both accessory and

433 malformed antlers, both of which had malformed antlers on the left side, 1 had accessory

434 antlers on the right side, the other buck had both accessory and malformed antlers on the

435 right side.

| Antler type | Location of the anomaly on the skull | | | Sum of all cases |
|---|---|---|---|---|
| | Left antler | Both antlers | Right antler | |
| Accessory | 5 | 2 | 9 | 16 (0.65%) |
| Broken | 14 | 0 | 12 | 26 (1.06%) |
| Malformed | 16 | 94 | 12 | 122 (4.96%) |
| Normal | | | | 2,294 (93.21%) |

436

437